# STRUCTURE & REPRODUCTION OF THE GYMNOSPERMS

## ( Fossil & Living )

★

TRIVEDI & SINGH

★

## CONTENTS

Chapter 1

# Introduction

The gymnosperms constitute a distinct subdivision of the Spermatophyta, the seed-bearing plants. The name 'Gymnospermae' is derived from two Greek words, gymnos=naked; sperma=seed. They are thus naked-seeded plants. Geological history reveals that the gymnosperms represent quite an ancient group of plants. Eames[1] keeps Gymnospermae between Filicineae and Angiospermae. According to him, the division Tracheophyta, which literally means tracheid-bearing plants, includes four subdivisions, namely, Psilopsida, Lycopsida, Sphenopsida and Pteropsida, the last includes the classes Filicineae, Gymnospermae and Angiospermae.

GENERAL CHARACTERS—Gymnosperms are predominantly woody plants with tree-like or shrubby habit. A few are climbing. Some of them are deciduous while others are evergreen. They are mostly xerophytic. *Sequoiadendron giganteum* Buchholz[2] is probably the tallest living tree reaching a height of nearly 100 metres with a girth of about 15 metres. Leaves are large and pinnate in cycads, and acicular or scale-like in conifers. The leaves borne on the gymnospermous plants may all be of one kind or of two kinds. Besides the foliage leaves, scale leaves are also present. Their arrangement may be spiral or cyclic. The leaves may be once compound as in *Cycas, Zamia*, etc., or twice compound as in *Bowenia*. In *Pinus* the leaves are modified into needles.

The vascular cylinder in the stem of gymnosperms is made up of collateral endarch and open vascular bundles arranged in a

1. **Eames, A. J.** 1936.
2. **Hui-Lin Li** 1952.

ring. There occurs a well-marked secondary growth. Pith and cortex both are much reduced in the conifers, hence the wood becomes densely packed or 'pycnoxylic'. In other gymnosperms like *Cycas* the cambial activity is short lived. In such cases the pith and the cortex are well-developed. Parenchyma in some quantity is present in the wood; the wood, therefore, is not so compact and it is called 'manoxylic'. It is observed that manoxylic wood occurs in the megaphyllous genera. They also have radially symmetrical seeds. Pycnoxylic wood occurs in the microphyllous genera with bilaterally symmetrical seeds. The vascular cylinder of the root is diarch to polyarch. Xylem is formed of tracheids possessing large, uniseriate or multiseriate bordered pits. Companion cells are said to be absent from the phloem of gymnosperms.

The reproductive organs in living gymnosperms, except the ovulate structures of *Cycas*, are arranged in the form of strobili or cones. The strobili may either be male (microsporangiate) or female (megasporangiate), rarely they are bisporangiate.

The ovule* is generally orthotropous, covered by a single envelope** (=integument); the latter may be differentiated into an outer fleshy (=outer sarcotesta), and inner fleshy (=inner sarcotesta) and a middle stony (=sclerotesta) layers. Inside the innermost layer of the envelope lies the nucellus, with a micropyle at the apex of the ovule.

The female gametophyte possesses two or more archegonia. Within the archegonium an egg or oosphere and a ventral canal nucleus are present but the neck canal cells are absent.

The male strobili (=cones) in general are smaller than the female ones and are short lived. Microsporophylls or stamens are broad and flat in *Cycas* but peltate in *Taxus* and *Dioon*.

Microsporangia or pollen-sacs are numerous and grouped in sori in *Cycas* but are reduced to two in *Pinus*. They are usually borne on the abaxial on the lower surface of the microsporophyll.

* Ovule = an indehiscent megasporangium, possessing a single functional megaspore and protected by one or more envelopes.

** Envelope = integument, made up of 2–3 (rarely 4) distinct layers.

The male gametophyte of *Cycas* has only one and that of *Ginkgo* and *Pinus* two prothallial cells. The pollen tube grows through the tissue of the female gametophyte and reaches the archegonium. Fertilization takes place and a zygote is formed by the fusion of the male and the female nuclei.

Only a part of the zygote develops into an embryo. Such a development of the embryo is spoken of as 'meroblastic'. The embryo later gets differentiated into upper (haustorial), middle (suspensorial) and basal (embryonal cells). Sometimes several embryos arise inside a seed. Such a phenomenon, called 'poly-embryony', occurs in *Pinus*. Embryo is usually straight. It is later (differentiated) into stem, leaf and root. Radicle is directed towards the micropyle and the plumule opposite it.

A true fruit, like that of the angiosperms, is not formed in the gymnosperms. Cotyledons are only 2 in *Cycas* but numerous in *Pinus* and these become green while still enclosed within the seed.

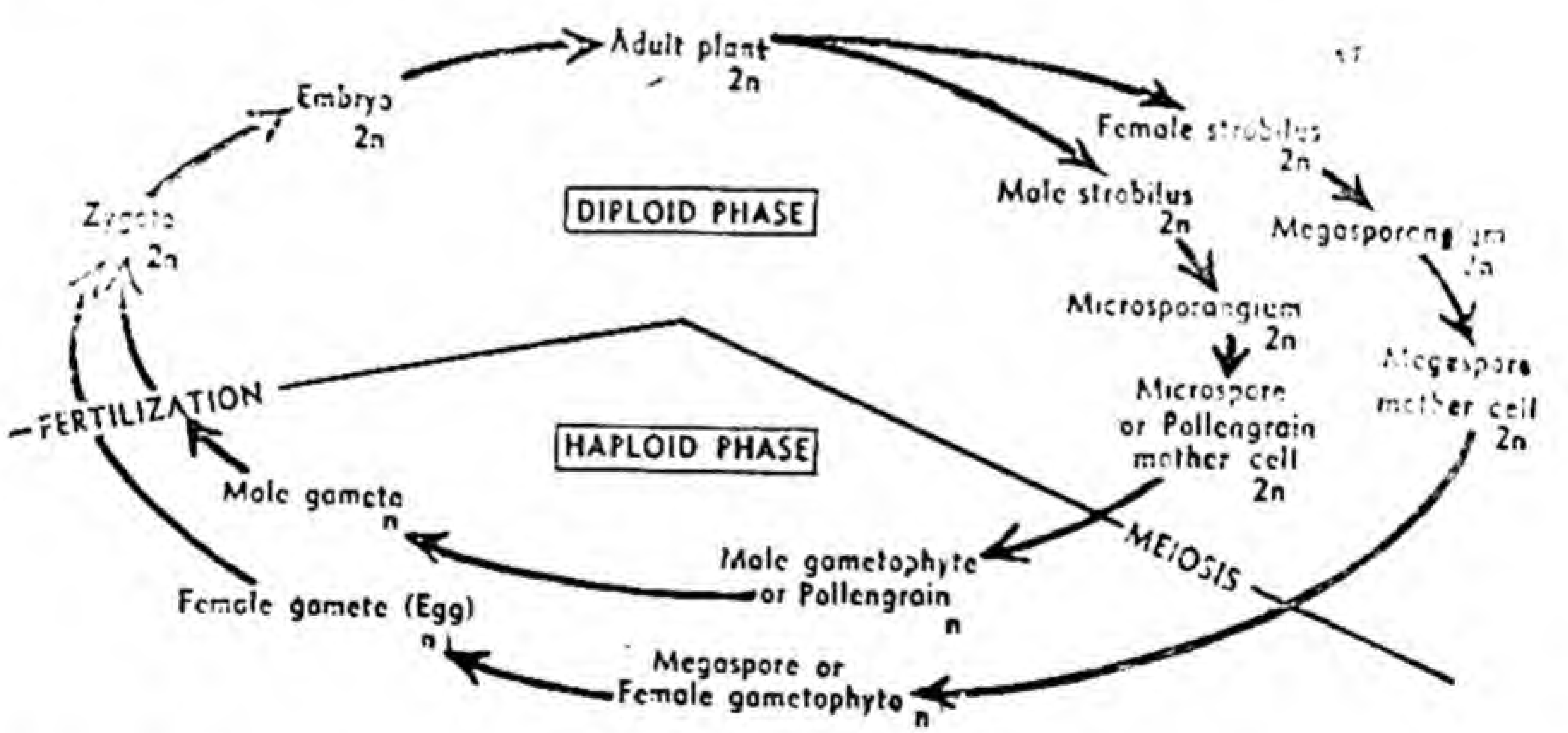



Fig. 1—1. Graphic representation of life-cycle of a typical gymnospermous plant.

In the gymnosperms, the seed-coat ruptures, the radicle comes out, gradually the seed develops and a young seedling is formed. The radicle grows downwards to form the primary tap root, while the plumule grows upright and forms the stem. The growth of stem is limited in *Welwitschia* while in others it continues to grow for a long time.

Gymnospermous plants have dominant and independent sporophyte (diploid) but a dependent and rudimentary gametophytic (haploid) phase (Fig. 1-1).

Sixteen genera and fifty-two species of living gymnosperms (including the Gnetales) are recorded from India[1].

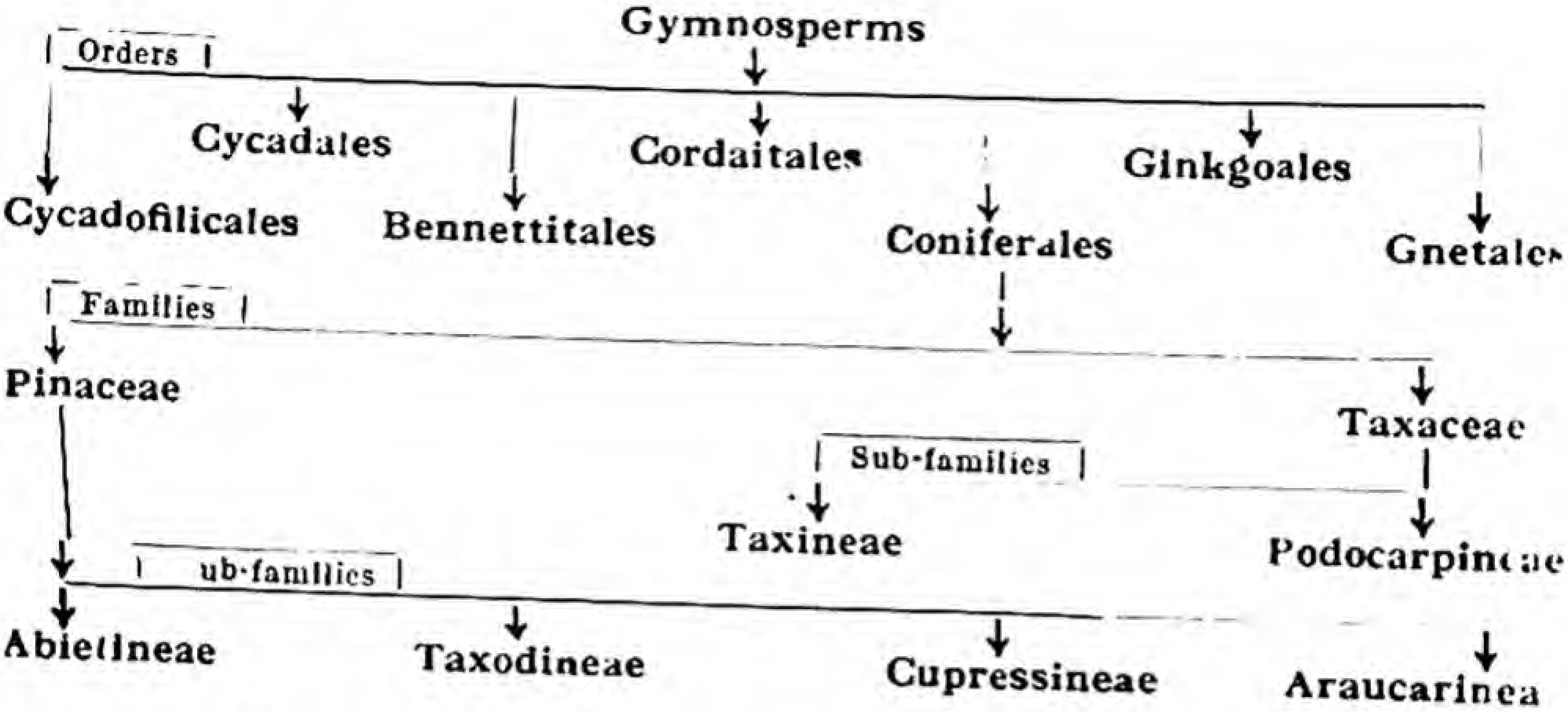
| Names of genus | Number of species |
|---|---|
| *Abies* Miller | 5 |
| *Cedrus* Trew | 1 |
| *Larix* Miller | 1 |
| *Picea* A. Dietrich | 3 |
| *Pinus* Linn. | 6 |
| *Tsuga* Carr. | 2 |
| *Cephalotaxus* Siebold & Zucc. | 2 |
| *Cupressus* Linn. | 1 |
| *Cycas* Linn. | 5 |
| *Juniperus* Linn. | 7 |
| *Libocedrus* Endl. | 1 |
| *Podocarpus* L' Hérit. ex. Pers. | 4 |
| *Taxus* Linn. | 1 |
| *Taiwania* Hayata | 1 |
| *Ephedra* Linn. | 7[2] |
| *Gnetum* Linn. | 5[3] |

CLASSIFICATION—The classification of gymnosperms has been quite a controversial subject because several genera and a few orders like the Cordaitales and the Cycadeoidales are known only in fossil state. Attempts have, however, been made from time to time by several botanists to classify them, some of the more important classifications are given below :

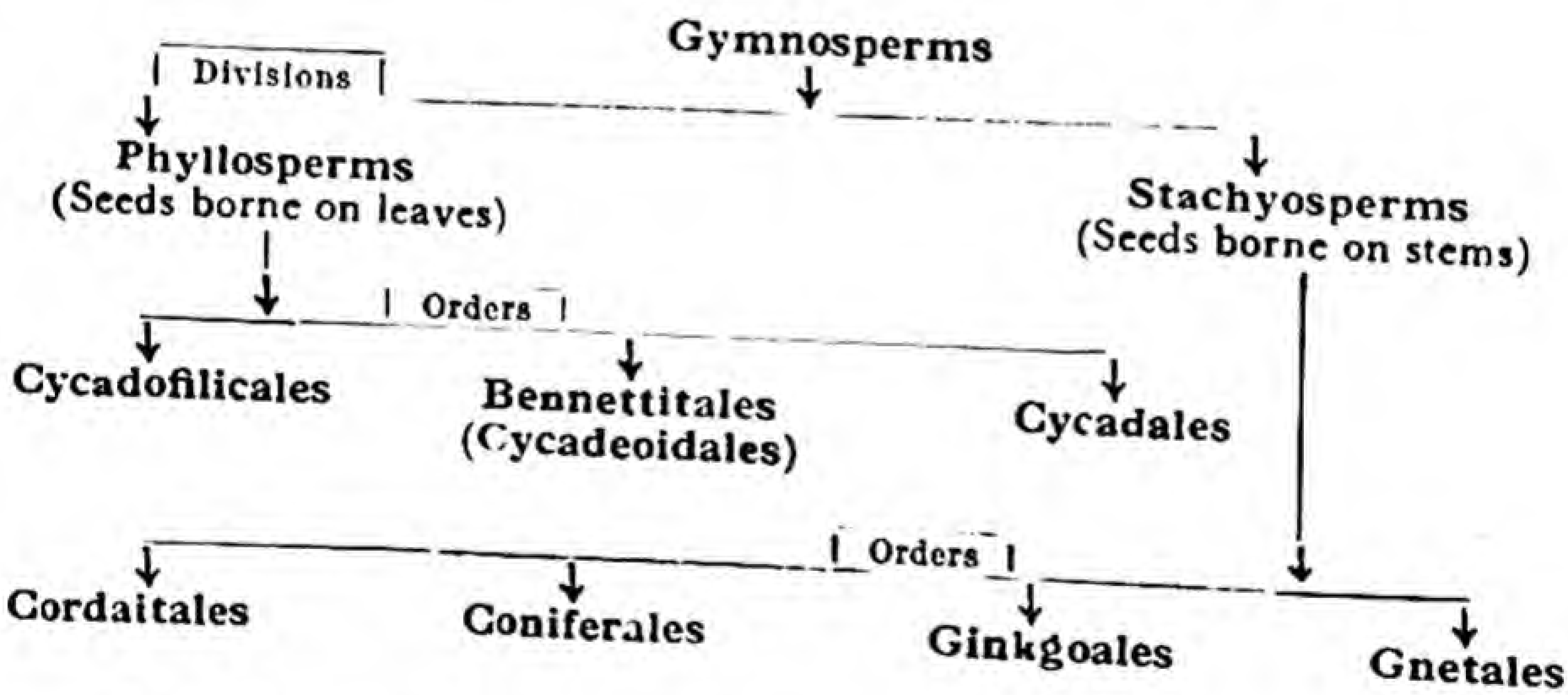
(1) Coulter and Chamberlain[4] have divided the gymnosperms into seven orders namely, Cycadofilicales, Cycadales, Bennettitales (Cycadeoidales), Cordaitales, Coniferales, Ginkgoales and Gnetales. The order Coniferales has been divided into two

1. Raizada, M. B. & K. C. Sahni 1960
2. Bor, N. L. 1953
3. Maheshwari, P. 1961
4. Coulter, J. M. & C. J. Chamberlain 1910.

families, viz., Pinaceae and Taxaceae. The former was subdivided into four and the latter into two sub-families as shown below :




(2) Sahni[1] divided the gymnosperms into two divisions namely Phyllosperms and Stachyosperms. The former was subdivided into three and the latter into four orders as below :




(3) Pant[2] has proposed a classification in which gymnospermous plants have been placed in three divisions, namely Cycadophyta, Chlamydospermophyta and Coniferophyta. The divisions Cycadophyta and Coniferophyta are subdivided into four classes each, while Chlamydospermophyta into a single class.

1. Sahni, B. 1920
2. Pant, D. D. 1957

The classes are further subdivided into 14 orders as shown below :

**Gymnosperms**

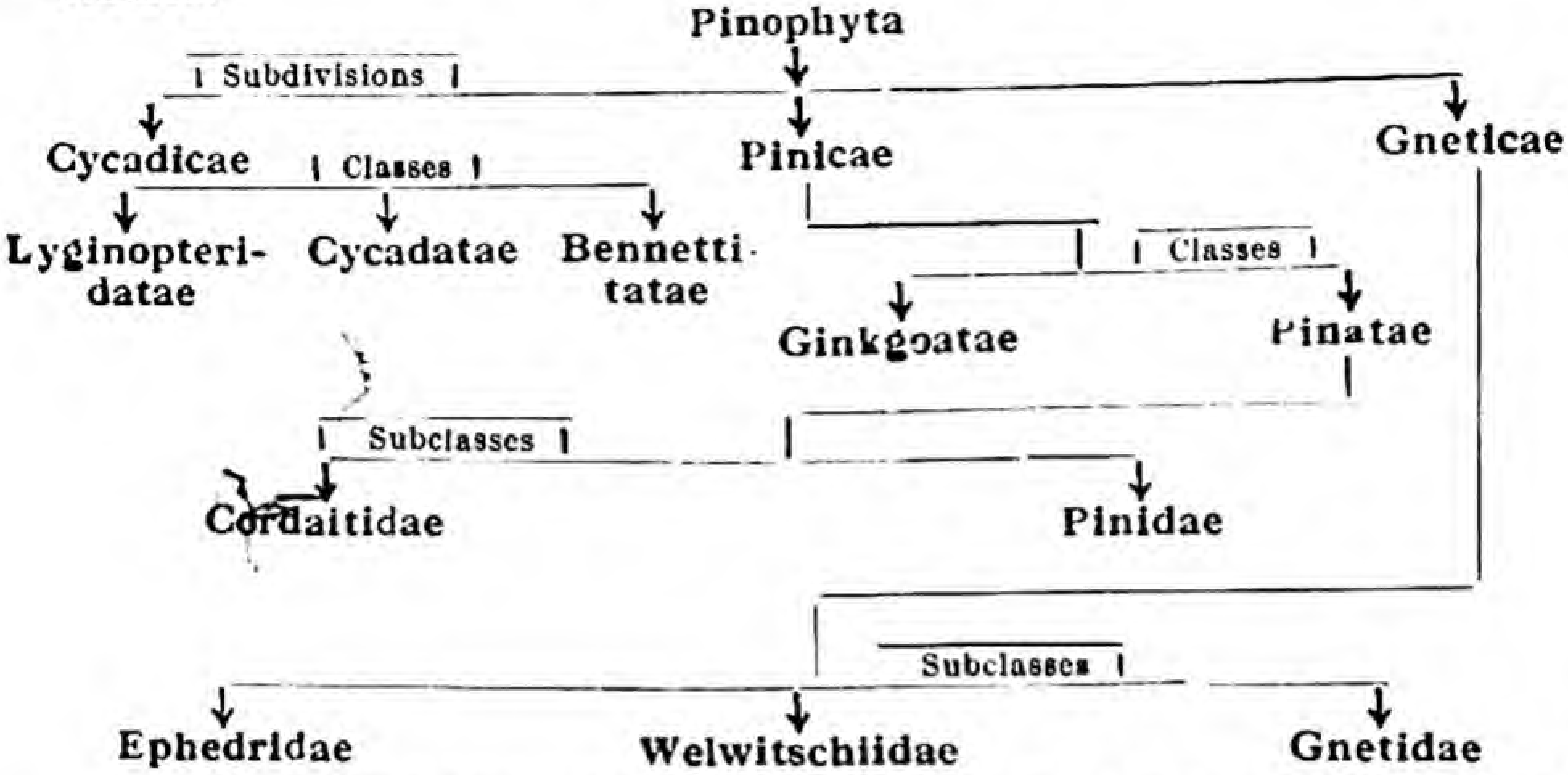
- Divisions
  - **Cycadophyta**
    - Classes
      - **Pteridospermopsida**
        - Orders
          - Lyginopteridales
          - Medullosales
          - Glossopteridales
          - Peltaspermales
          - Corystospermales
          - Caytoniales
      - **Cycadopsida**
      - **Pentoxylopsida**
      - **Cycadeoideopsida**
  - **Chlamydospermophyta**
    - Class
      - **Gnetopsida**
        - Orders
          - Gnetales
          - Welwitschiales
  - **Coniferophyta**
    - Classes
      - **Coniferopsida**
        - Orders
          - Cordaitales
          - Coniferales
          - Ginkgoales
      - **Ephedropsida**
        - Order
          - Ephedrales
      - **Czekanowskiopsida**
        - Order
          - Czekanowskiales
      - **Taxopsida**
        - Order
          - Taxales

(4) Raizada and Sahni[1] classify the gymnosperms into eight orders namely, Pteridospermales (=Cycadofilicales), Cycadeoidales (=Bennettitales), Cycadales, Pentoxylales, Cordaitales, Ginkgoales, Coniferales and Gnetales. Out of these, the first three belong to the cycadophytes and the last four to the coniferophytes. The position of the Pentoxylales is, however, uncertain.

(5) Cronquist, Takhtajan and Zimmermann[2] have recently proposed a classification in which the subkingdom, Embryobionta (=embryo-bearing plants) has been split into eight divisions namely, Rhiniophyta, Bryophyta, Psilotophyta, Lycopodiophyta, Equisetophyta, Polypodiophyta, Pinophyta, and Magnoliophyta.

1. Raizada, M. B. & K. C Sahni, 1960
2. Cronquist, A., A. Takhtajan, & W. Zimmermann 1966

Pinophyta includes the gymnospermous plants which is further divided into the following subdivisions, classes and sub-classes:




DISTINGUISHING FEATURES OF THE DIFFERENT ORDERS —The different orders of the gymnosperms (fossil and living ones) are characterised as under :

**Pteridospermales**—Plants with fern-like foliage, stem slender sporangia on frond-like leaves, but never grouped in a definite strobilus; Palaeozoic-Mesozoic.

**Cycadeoidales**—Trees with stems covered with an armour of persistent leaf-bases. Microsporophylls frond-like forming a loose crown. Megasporophylls no longer leaf-like, but forming a specialized strobilus-like structure; Mesozoic.

**Cycadales**—Plants with palm-like habit; micro- and megasporophylls grouped into strobili except in *Cycas* where the megasporophylls are loosely arranged but the microsporophylls are aggregated to form a strobilus. Male cells motile; Mesozoic to present day.

**Ginkgoales**—Medium sized trees; leaves flattened and lobed in various ways with dichotomous venation. Male and female reproductive structures collected into strobili; male cells motile and multiflagellate; Palaeozoic to present day.

**Pentoxylales**—Low shrubs; females infrutescence consisting of numerous strobili spirally attached on a peduncle, each bearing numerous ovules on a central axis with no megasporophylls,

ovuliferous scales or interseminal scales. "Male organs consist of branched sporangiophores which are arranged in a whorl, these fuse basally to form a disc; Jurassic.

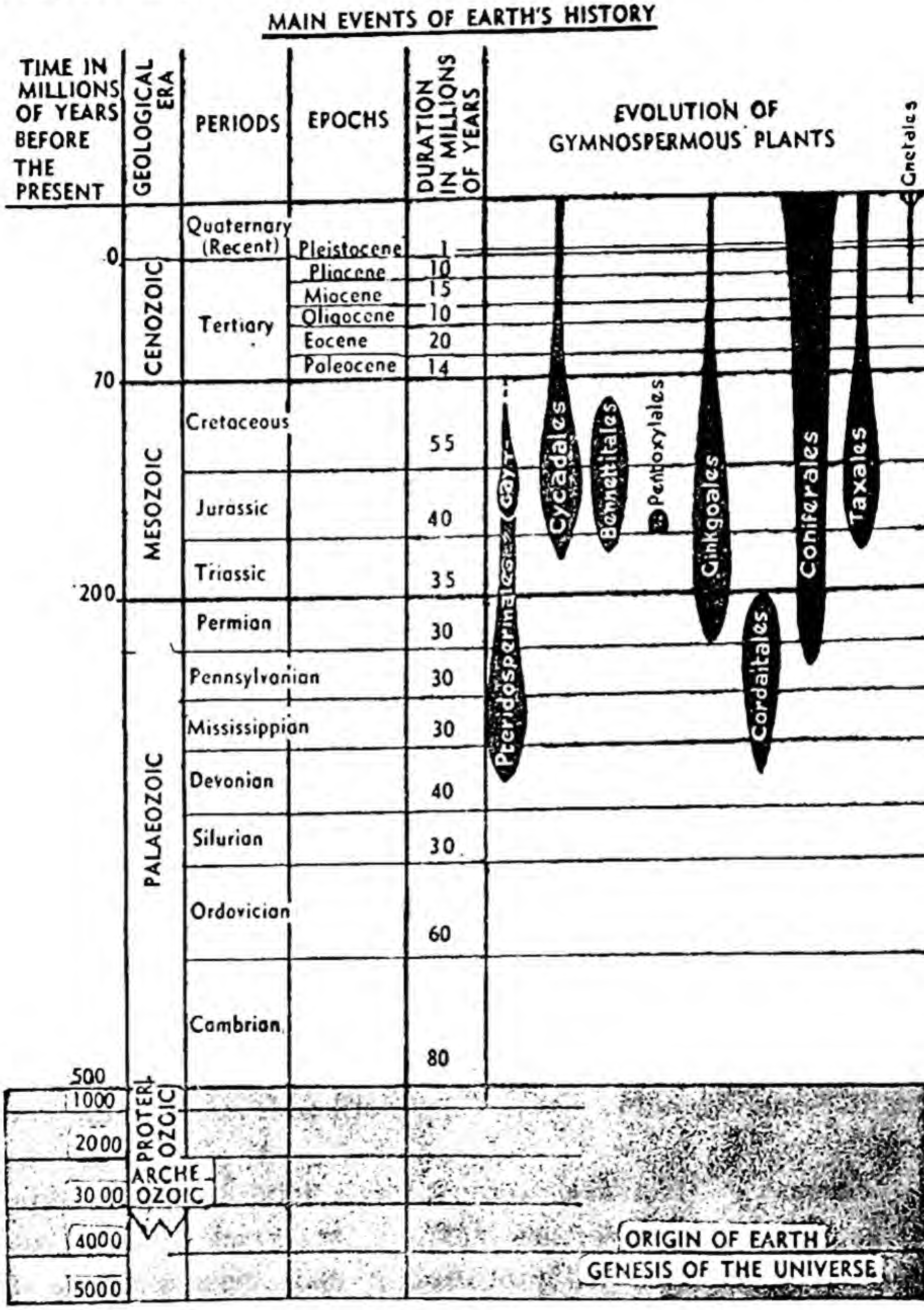



Fig. 1—2 Geological history of the gymnospermous plants.

**Cordaitales**—Large trees with flat strap-shaped leaves, fructifications in strobili; Palaeozoic.

**Coniferales**—Large trees or shrubs; leaves needle or scale-like, sometimes flattened; male cells never motile and male flowers arranged in more or less compact cones; Palaeozoic to present day.

**Taxales**—Evergreen shrubs or trees; leaves in spirals, wood pycnoxylic, tracheids with tertiary spirals; resin canals absent; Ovules solitary with an aril; male flowers consisting of sterile scales or whorled sporophylls, each with 2-8 pollen sacs; embryo with 2 cotyledons. Triassic to present day.

**Gnetales**—Small trees, shrubs or climbing shrubs; leaves—opposite, embryo dicotyledonous. Strobili compound in both the male and the female plants; recent with hardly any known fossil history.

**AFFINITIES OF THE GYMNOSPERMS**

The gymnosperms bear close affinities with the Filicineae on the one hand and the Angiosperms on the other, while in many other characters they are different from both.

**Resemblances with the Filicineae**—The sporophytic and the gametophytic generations in both the groups are alternate but there is reduction in the gametophytic generations of the gymnosperms. Here the gametophyte is reduced and is unlike that of the ferns as it is totally dependent upon the sporophyte. There occurs gradual increase in the complexity of the sporophyte as it differentiates into root, stem and leaf. .he cycads, a group of gymnosperms, resemble the ferns further in the compound nature of their leaves and in circinate vernation. Gymnosperms and ferns are alike in the absence of companion cells from the phloem, and vessels from the xylem of all gymnosperms, except the Gnetales where the vessels are present. Gymnosperms resemble *Selaginella*, *Isoetes*, *Marsilea* and some fossil ferns in the presence of small microspores and large-sized megaspores, i. e., in showing heterospory. Endosperm, or the female prothallus, develops before fertilization from the tisue of the female gametophyte. Multiflagellate and motile antherozoids are present both in the Cycadales and the pteridophytes, but in other gymnosperms like the Coniferales and the Gnetales they are non-flagellate.

**Differences from the Filicineae**—Gymnosperms are comparatively more xerophytic than most of the ferns. Development of tap root system is conducive to better anchorage and absorption. There is excessive secondary growth in the higher gymnosperms. Seed-habit, which predominates in the gymnosperms and the angiosperms, perhaps helps the plants in tiding over unfavourable circumstances. It was only nascent in the fossil pteridophytes but does not occur in the living ones. Pollen grains are light, and develop partly before their release from the microsporangium. Fertilization is truly siphonogamous or siphonogamy may be combined with zooidogamy as in *Cycas* where the pollen tube is haustorial in nature. There is permanent retention of female gametophyte inside the megaspore in the gymnosperms. In the archegonium of the gymnosperms there is absence of neck canal cells and frequent elimination of ventral canal cell. In *Gnetum* and *Welwitschia* even the archegonia are absent.

**Resemblances with the Angiosperms**—Shrub or tree-like habit is common to both the groups. Formation of flower like structures by the aggregation of sporophylls in strobili in more highly evolved gymnosperms is comparable to apetalous flowers of the angiosperms. Presence of pollen tube, for carrying the male gametes to the egg (siphonogamy) is a common feature. Retention of megaspore inside the megasporangium and its further development into female gametophyte while still attached to the mother plant, is a character common to both.

The ovule is surrounded by an envelope divisible into the outer and inner fleshy and middle stony layers except in the Gnetales where the envelope is 2-3 rarely 4 layered to ensure better protection of the seed.

**Differences from the Angiosperms**—Ovules are not enclosed within an ovary in the gymnosperms. Vessels are absent from the wood of gymnosperms except from that of the Gnetales. Sieve tubes and companion cells are absent in the phloem which in the gymnosperms consist of sieve cells and phloem parenchyma. The stigma and style, though present in the angiosperms are

absent from all gymnosperms and the pollen grains enter the ovules directly through a micropylar canal. Pollination is mostly anemophilous in the gymnosperms while in the angiosperms it may be effected by various agencies Coloured bracts, perianth, and nectaries, etc, are absent in the gymnosperms. Sporangia are borne on leaf-like structures which are aggregated in the form of strobili except in female *Cycas*. Archegonia are present in the ovules of all gymnosperms except those of *Gnetum* and *Welwitschia* but they do not occur in angiosperms at all. Prothallial cell or cells are present in the pollen grains of all gymnosperms; except perhaps *Gnetum*; they are absent from the angiosperm pollen. Endosperm formation is a pre-fertilization phenomenon except in *Gnetum*, where it is somewhat concurrent with fertilization. In angiosperms, endosperm-formation is a post-fertilization phenomenon. Double fertilization or triple fusion does not occur in gymnosperms, but is present in the angiosperms. Occurrence of free-nuclear divisions in zygote is a primitive feature found only in the gymnosperms but not in the angiosperms.

The gymnosperms, therefore, form a distinct group of plants. They differ from the Filicineae and the Angiosperms in some characters. On the other hand, they share many characters with both these classes. They thus constitute an independent group of plants.

Chapter 2

# Pteridospermales
## (Cycadofilicales)

The Pteridospermae Oliver and Scott (=Cycadofilicales Potonié) constitute the popularly known 'seed-bearing plants with fern-like foliage, or, seed-ferns'. Arnold[1] divides the pteridosperms into 5 families, and one order viz., Lyginopteridaceae, Medullosaceae, Calamopityaceae Peltaspermaceae Corystospermaceae and the caytoniales. Pant[2] makes a distinct class Pteridospermopsida for these plants and divides them into six orders namely, Lyginopteridales, Medullosales, Glossopteridales, Peltaspermales, Corystopermales and Caytoniales. The pteridosperms flourished in the Palaeozoic, though the representatives of the last four orders continued into the Mesozoic. Our knowledge of the representatives of this class is based chiefly on fragmentary fossil remains which constitute various form-genera.

DISTINGUISHING FEATURES—Pteridosperms are supposed to be intermediate in character between the ferns and the cycads. They may be distinguished from these two by the following features:

The pteridosperms possessed slender stems with large, fern-like fronds or leaves as represented by *Alethopteris* Stern., *Neuropteris* (Brongn.) Stern., *Sphenopteris* (Brongn.) Stern., etc. The cuticle of leaves and branches resembled to that of the cycads in being resistant to oxidative maceration. Stele was protostelic or siphonostelic, rarely it was polystelic. The stem usually possessed mesarch primary vascular bundles. Secondary growth took place resulting in the formation of secondary xylem and phloem. Cortex was wide and had longitudinally aligned fibre-strands Leaf-traces were large and were composed of one or more vascular strands. Secondary wood was soft, manoxylic and the tracheids had multiseriate bordered pits on their radial walls. The male reproductive organs were probably clustered at the apices in the form of

1. Arnold, C. A. 1947.
2. Pant, D. D. 1957.

synangia which were sometimes quite complex. The pteridosperms bore seeds which were sometimes partially enclosed, in an envelope called 'cupule' as in *Lagenostoma* Williamson or completely enclosed as in *Physostoma* Williamson. The ovules and seeds were borne on ordinary fronds or on megasporophylls. Strobili have not been reported in any pteridosperm.

The following form-genera are described here :

| | |
|---|---|
| Stem | .. *Lyginopteris oldhamia* (Binney) H. Potonié |
| Rachis | .. *Rachiopteris aspera* Williamson |
| Root | ... *Kaloxylon hookeri* Williamson |
| Frond | ... *Sphenopteris hoeninghausi* Brongniart. |
| Pollen-bearing organs | ... *Crossotheca hoeninghausi* Brongniart Kidston |
| Seed | ... *Lagenostoma lomaxi* Oliver & Scott |

MORPHOLOGICAL FEATURES—The stem, *Lyginopteris oldhamia* was long and slender. It measured nearly 3 cm in diameter and possessed spirally arranged leaves. It is presumed that this plant, with delicate and weak stem, occurred in thickets, or it may have taken support of some other plant to spread out, as it was not possible for it to stand erect by itself.

The root, *Kaloxylon* was probably borne adventitiously.

The petiole *Rachiopteris aspera* had glands (fig. 2-4) which were similar to those borne on the seed envelope or cupule of *Lagenostoma lomaxi* (fig 2-6).

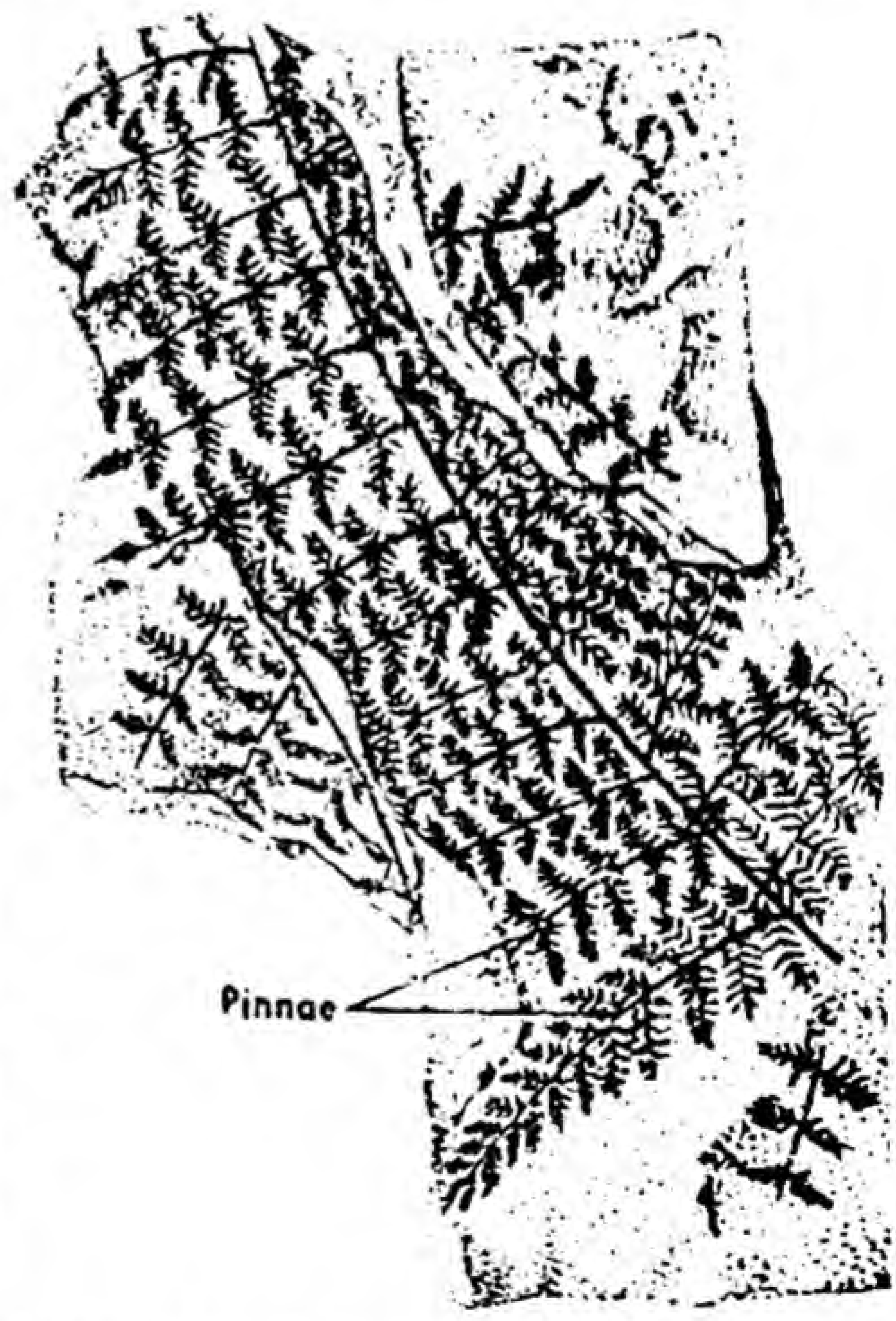


Fig. 2—1 A portion of the frond of *Lyginopteris oldhamia* showing habit and the arrangement of pinnae (Modified from Andrews).

The leaves *Sphenopteris hoeninghausi* measured nearly 50 cm in length. The rachis was dichotomously branched above and each dichotomy was

tripinnate. The pinnae were borne opposite each other at right angles to the rachis (fig. 2-1).

HISTOLOGICAL FEATURES—*Lyginopteris oldhamia* possessed large parenchymatous pith (fig. 2-2) with clusters of thick-walled cells, called 'sclerotic nests' scattered in it. Mesarch vascular bundles, 5-10 in number, surrounded the pith in the form of a ring. The bulk of the primary wood was centripetal, but centrifugal xylem was also well developed ; the primary xylem, therefore, had mesarch structure. Secondary wood formed a continuous ring round the primary xylem, which at places was interrupted by leaf-traces. It consisted of large tracheids with

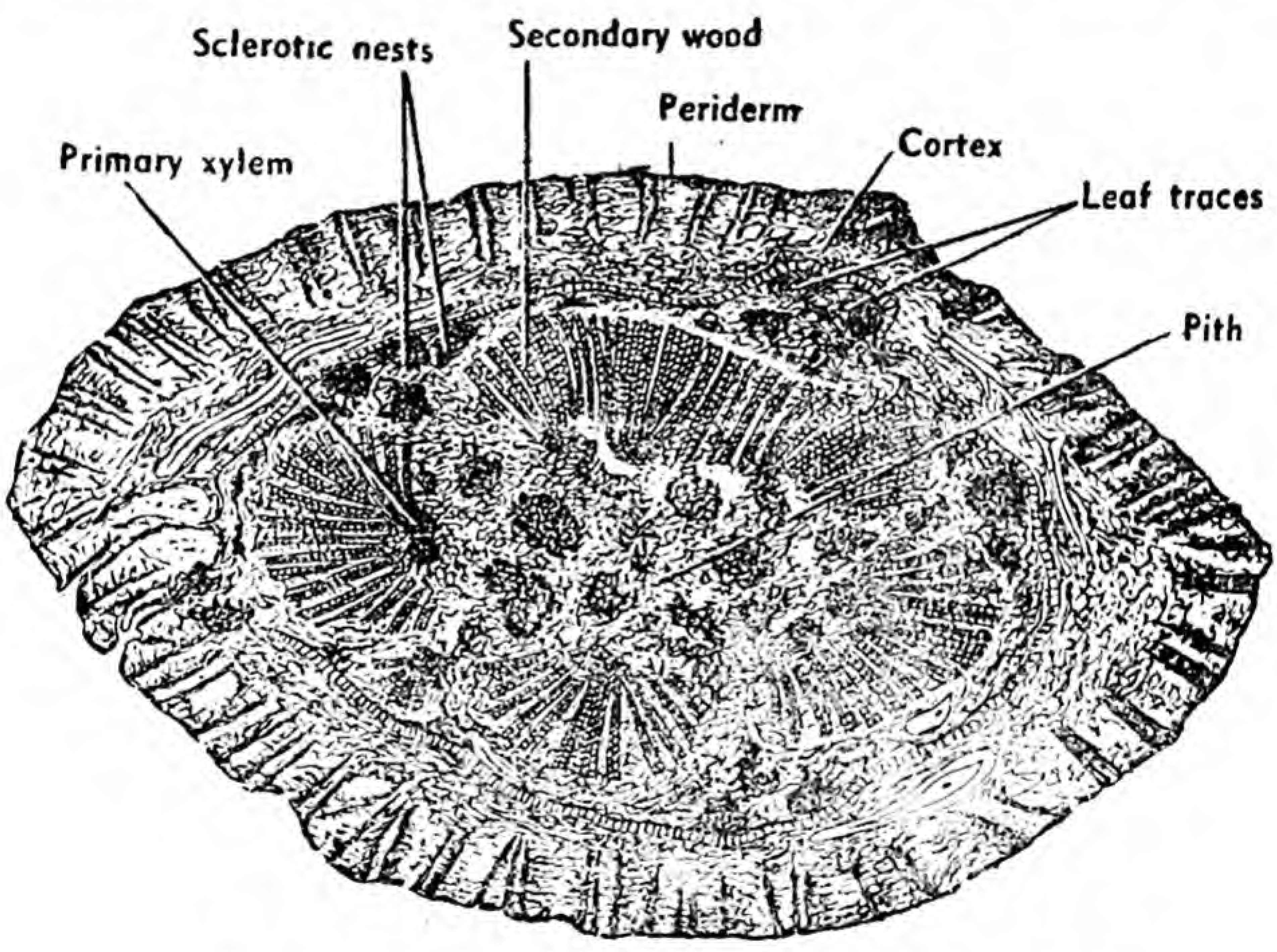



Fig. 2—2 T. S. of the stem of *Lyginopteris oldhamia* with well-developed secondary wood and leaf traces (After Williamson & Scott).

multiseriate bordered pits on their radial walls along with a large number of broad, many-celled high, medullary rays. Pits were irregularly distributed unlike those of the Cordaitales. Rays of secondary wood varied from a fraction of a mm to 2 cm in height and 1-12 cells in width.

Secondary wood on its outer side was surrounded by phloem and pericycle. Phellogen probably developed from the outer layers of pericycle and produced the periderm. The pericycle, like the pith, possessed a large number of 'sclerotic cells'. This inner cortex was parenchymatous in nature but the outer one possessed radially broadened fibrous strands which formed a vertical network (fig. 2-3). The 'windows' or 'meshes' of the network possessed parenchymatous cells.

Fig. 2—3 V.S. through the outer cortex of the stem of *Lyginopteris oldhamia* showing the network of sclerenchymatous strands (After Arnold).

The leaf-trace, at the point of its origin, started with a single protoxylem strand which later divided into two xylem strands, one of which, in the form of a reparatory strand, continued in the stem, while the other turned outwards and passed into the leaf base.

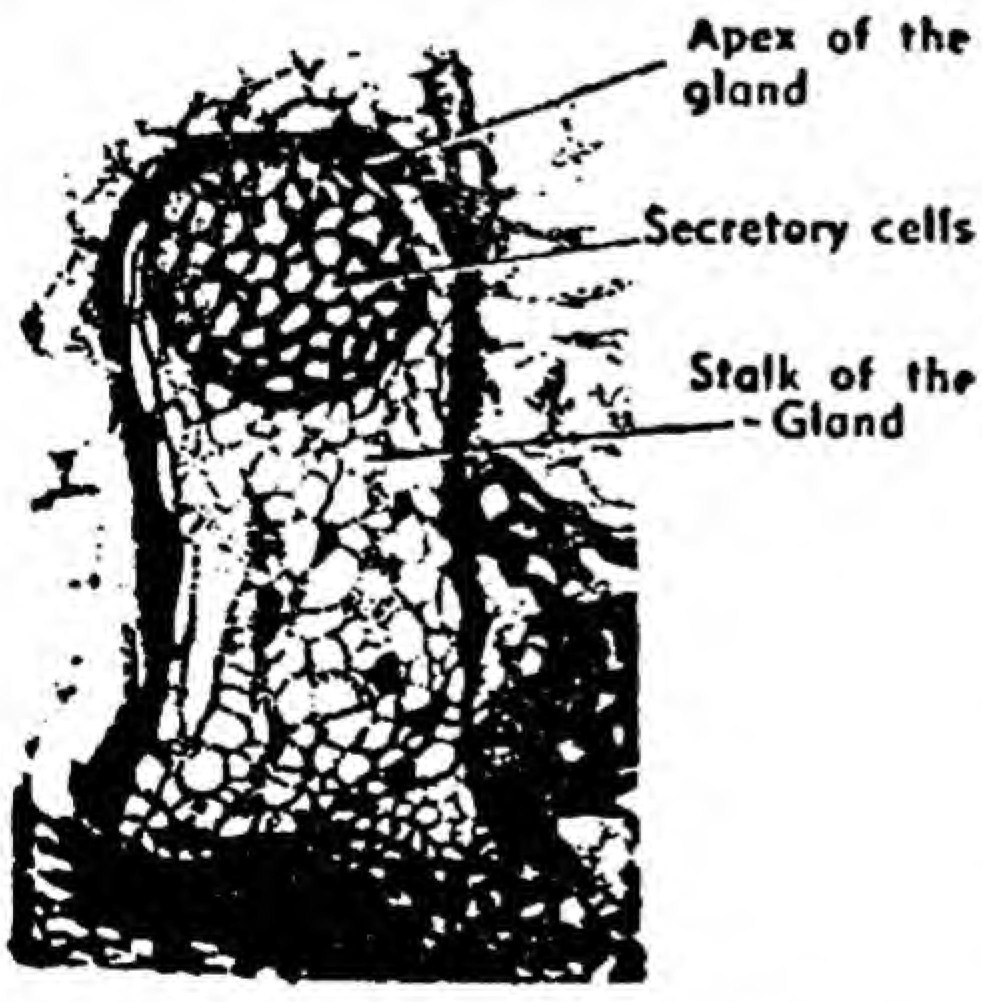


Fig. 2—4 A capitate gland of the rachis of *Lyginopteris oldhamia* (After Arnold).

*Kaloxylon* possessed radial vascular strands with exarch xylem which had spirally thickened tracheids. Cortex was divisible into thick and thin walled zones.

**LIFE-HISTORY**

The male and female reproductive organs are presumed to have been borne on two distinct individuals. The plants thus were probably dioecious.

The microsporangiate organ, known as *Crossotheca hoeninghausi*, possessed fertile pinnules. Each pinnule bore 6 or more pendant, bilocular microsporangia (fig. 2-5). A microsporangium measured nearly 3 mm. in length and 1 mm. in breadth. It contained microspores which were 50-70$\mu$ in diameter. Sporangia probably dehisced like those of *Selaginella* or *Isoetes*.

The seed, *Lagenostoma lomaxi*[1] remained partially closed in a lobed husk or 'cupule' (fig. 2-6). The latter possessed glands (figs. 2-4&2-6) on the exterior, these were identical to those present on *Rachiopteris aspera* (fig. 2-4), the axis. The ovule was barrel-shaped, it was radially symmetrical and measured nearly 5·5 mm. in length and 4·25 mm. in breadth. The envelope of the ovule was traversed by nine vascular strands.

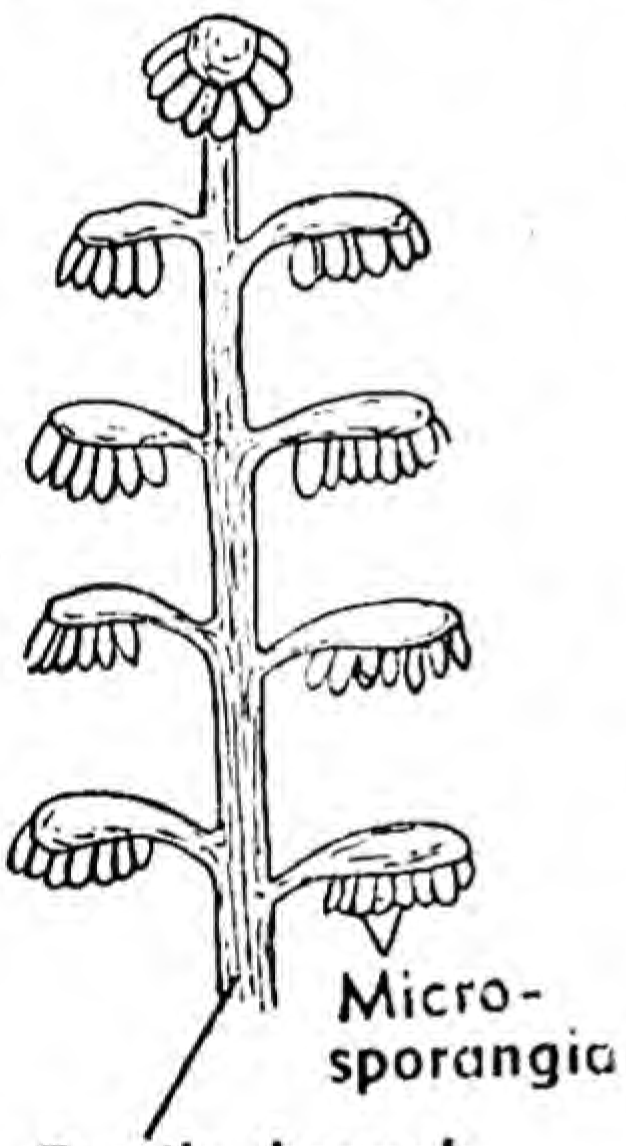



Fig. 2—5 *Crossotheca sp.* the male reproductive structures of *Lyginopteris oldhamia* with pendant microsporangia (After Arnold).

Long [2,3] while describing many genera and species of pteridosperms from lower carboniferous observed that in some the ovules were borne directly on a lax branching system. In these, protection to ovule was afforded by a system of branches as in *Eurystoma* which had no cupule. In *Stamnostoma* the branching system closely invests one or more ovules. *Calathospermum* has a definite cupule. The fossil evidence available goes to show that the cupule is morphologically a frond or its part and further that cupules and integuments are morphologically comparable structures Walton[4] thinks that

1. Oliver, F. W. & D. H. Scott 1904.
2. Long, A. G. 1960.
3. ,, ,, 1961.
4. Walton, J. 1960.

the ovules of *Genomosperma* and *Stamnostoma* were probably pendant at the time of pollination.

GAMETOPHYTIC GENERATION—Not much is known about the male gametophytes or microspores except that they have been found inside the pollen chamber of *Lagenostoma ovoides* Williamson[1] in large numbers. Each microspore possessed two walls, the outer called exine, and the inner intine. The spores probably germinated in the pollen chamber.

The female reproductive body known as *Lagenostoma lomaxi* (fig. 2-6) consisted of centrally situated nucellus which was free at its apex (fig. 2-7). The megaspore membrane was simple in structure resembling the exine of the pteridophytic spores[2]. It also possessed a thick stout envelope which was provided with nine vascular strands. Pollen chamber was present at the apex of the nucellus. Long[3] reported the presence of several archegonia near the micropyle.

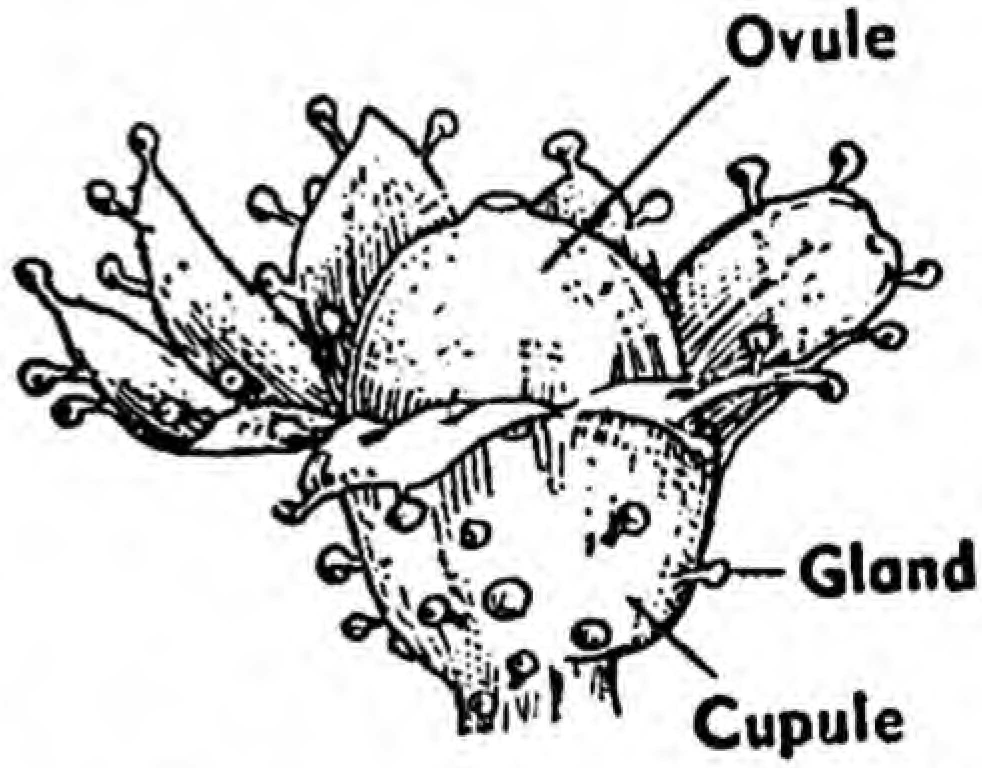


Fig. 2—6 *Lagenostoma lomaxi*, the seed of *Lyginopteris oldhamia* enclosed in a glandular cupule (After Scott).

OTHER FORM GENERA OF THE FAMILY—*Callistophyton poroxyloides* Delevoryas, *Schopfiastrum decussatum* Andrews, *Heterangium grievii* Will. are stems and *Tyliosperma orbiculatum* Mamay, *Physostoma elegans* Will., are seeds usually referred to the family Lyginopteridaceae.

ORIGIN AND AFFINITIES—Beck[4] suggests that the cycadophytic and coniferophytic gymnosperms, placed under a

1 Benson, M. 1908.
2. Pettit, J. M. 1966.
3. Long, A. G. 1944.
4. Beck, B. C. 1966

single division Pinophyta[1], might have a common origin in the Aneurophytales. The cycadophytes have probably evolved through the calamopityeans and the coniferophytes through *Archaeopteris* or such other genera.

Regarding the affinities of Pteridosperms, Eames[2] suggests that the resemblances between the ovules of Pteridosperms and Angiosperms may be considered merely of superficial nature and the bitegmic nature of the pteridosperm seed is of little importance. The Pteridosperms, however, resemble the ferns and the gymnosperms in the following respects :

RESEMBLANCES WITH FERNS

The pteridosperms are seed-bearing plants. Their male reproductive organs (fructifications) can be compared to those of the present day Marattiaceae. The protostelic or siphonostelic nature of stele as well as the form of frond are similar to those of the ferns. The name *Cycadofilices* as proposed by Potonié[3] for the fossilised stems possessing transitional characters between the ferns and the seed-plants is based on this fact.

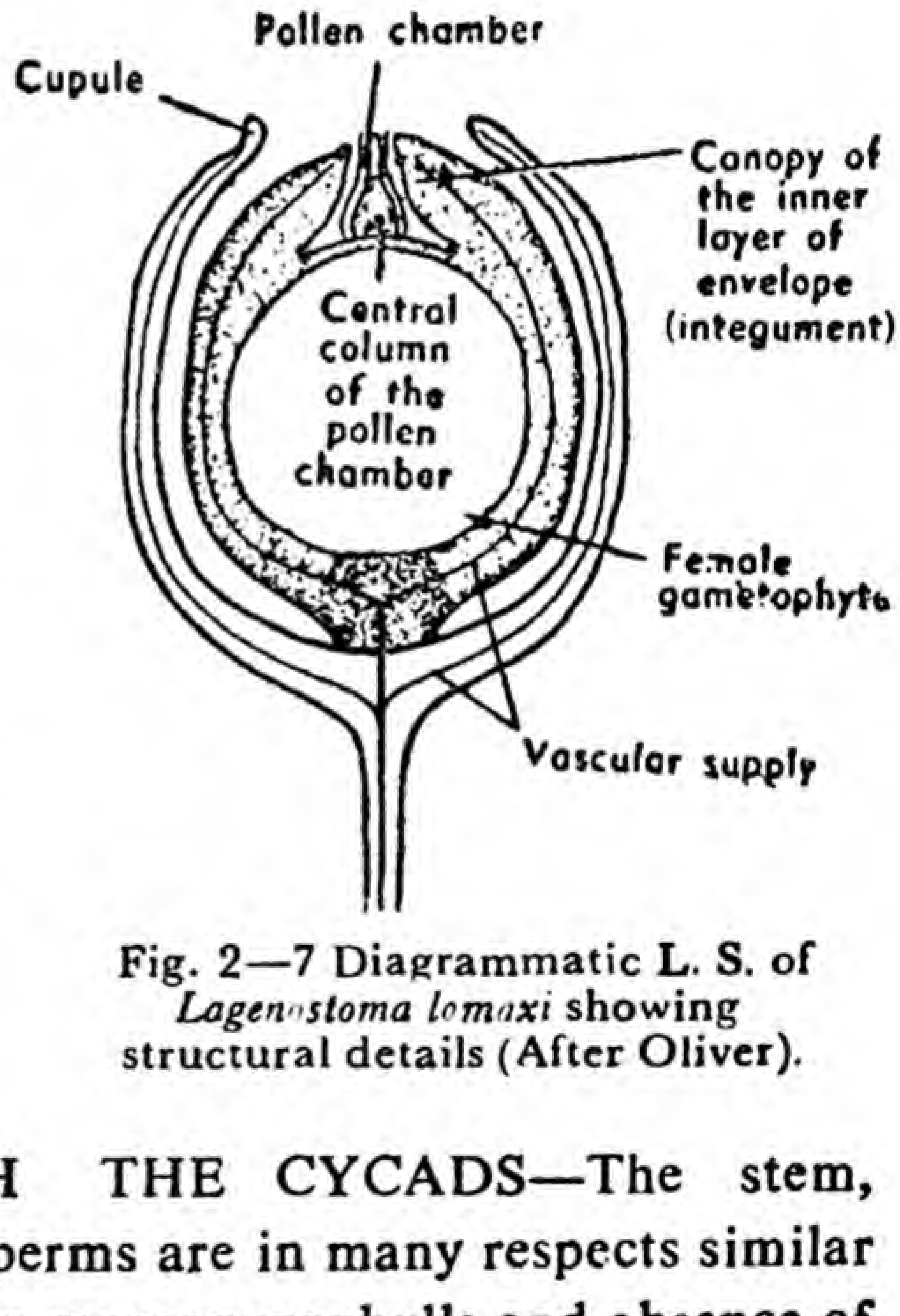



Fig. 2—7 Diagrammatic L. S. of *Lagenostoma lomaxi* showing structural details (After Oliver).

RESEMBLANCES WITH THE CYCADS—The stem, petiole and seeds of the pteridosperms are in many respects similar to those of the cycads. Leaf-like megasporophylls and absence of a well-organised female strobili, as in *Cycas*, is a character common to both. Hence some morphologists consider the pteridosperms as 'the cycads without strobili'.

1. Cronquist, A. A., Takhtajan, W. Zimmermann 1966.
2. Eames, A. J. 1936.
3. Potonié, H. 1902.

Chapter 3

# Cycadeoidales

## (= Bennettitales)

The cycadeoids were cycad-like plants which are now extinct. They have been considered to form a distinct class, the Cycadeoideopsida of the division Cycadophyta[1]. The order flourished from the Triassic to the Lower Cretaceous. Because of this restricted geological range, these plants are commonly called 'the Mesozoic cycadophytes'.

DISTINGUISHING FEATURES—The cycadeoid stems were provided with a wide pith and manoxylic wood. The leaves were mostly pinnate-compound like those of the living cycads and they had an open venation. Rarely they were simple with closed venation. The epidermal cells had sinuous walls while those of the living cycads have straight walls. The guard cells surrounding the stoma were flanked by a pair of subsidiary cells which are supposed to have originated from the same mother cell that gave rise to guard cells their development is thus said to have been syndetocheilic. In the living cycads, on the other hand, it is haplocheilic. Stomata in the Cycadeoidales were generally oriented transversely to the longer axis of the leaf. Reproductive organs were organised in the form of strobili called "flowers", superficially resembling those of the angiosperms. The plants were generally monoecious, i. e. both the microsporangia and the megasporangia were present on the same plant. The microsporophylls (=stamens) surrounded a central ovuliferous (=megasporangiate) receptacle. Ovules were stalked and numerous; they were borne on a conical, cylindrical or dome-shaped receptacle which also bore interseminal scales. The scales were more or

1. Pant D. D. 1957.

less united to form a shield. Male reproductive organs were borne in a whorl, they were free or fused, entire or pinnate. Microsporangia were borne in the form of synangia. Seeds possessed only 2 cotyledons.

The fossilised trunk, *Bucklandia* Presl. was the first specimen of this order which was collected from Great Britain in 1825. Since then several other genera and species have been collected and described from Europe, America, India, etc.

CLASSIFICATION—The order Cycadeoidales (=Bennettitales) has been divided into three families[1] namely, Cycadeoidaceae, Williamsoniaceae and Wielandiellaceae. They are distinguished from one another by the following characters :

The members of the Cycadeoidaceae possessed ovoid or short columnar trunk which was thickly armoured. The cycadeoid flowers (=fructifications) were borne laterally on the trunk and these remained partially sunken within the leaf-bases. The members of this family generally occur as petrifactions. *Cycadeoidea* Buck is the best studied genus of the family.

The members of the Williamsoniaceae possessed slender unbranched trunk, like the cycads which rarely produced lateral branches. The flowers of the Williamsoniaceae were either sessile or stalked. They were never embedded in the thick ramentum of leaf-bases and scales like those of the Cycadeoidaceae. The members of the Williamsoniaceae have been mostly preserved in the form of impressions or compressions. *Williamsonia* Carr. is the best known genus of the family.

The members of the Wielandiellaceae possessed slender and forked stems ; they thus differed from both the above families. In *Wielandiella* Nathorst female flowers were borne in the fork of the branches. The latter possessed unipinnate-compound leaves, *Anomozamites nilssoni*. The other genus, *Williamsoniella* Thomas possessed hermaphrodite flowers and simple leaves, *Nilssoniopteris* Nath.

1. Sporne, K. R. 1965.

## *CYCADEOIDEA* Buckland

The generic name *Cycadeoidea* Buckland was for the first time employed for the petrified trunks from the Isle of Wight. *Cycadeoidea etrusca* was one of the earliest known plants of this order. It was discovered from an Etruscan tomb in 1867. Many European palaeobotanists prefer to call *Cycadeoidea* as *Bennettites*. As there is no structural difference between the two and because *Cycadeoidea* was the first name proposed, it has been used here [1&2].

MORPHOLOGICAL FEATURES—The cycadeoid trunks were subspherical, oval or columnar in shape, their diameter varied from a few centimeters to even sixty centimeters (fig. 3-1). More than 30 species of *Cycadeoidea* have been described from the upper Jurassic to the upper Cretaceous. Some of them attained a height of 3.0 to 3.6 metres while others were comparatively short. Plants showed a thick armour of leaf-bases. Branching was rare as in the living cycads.

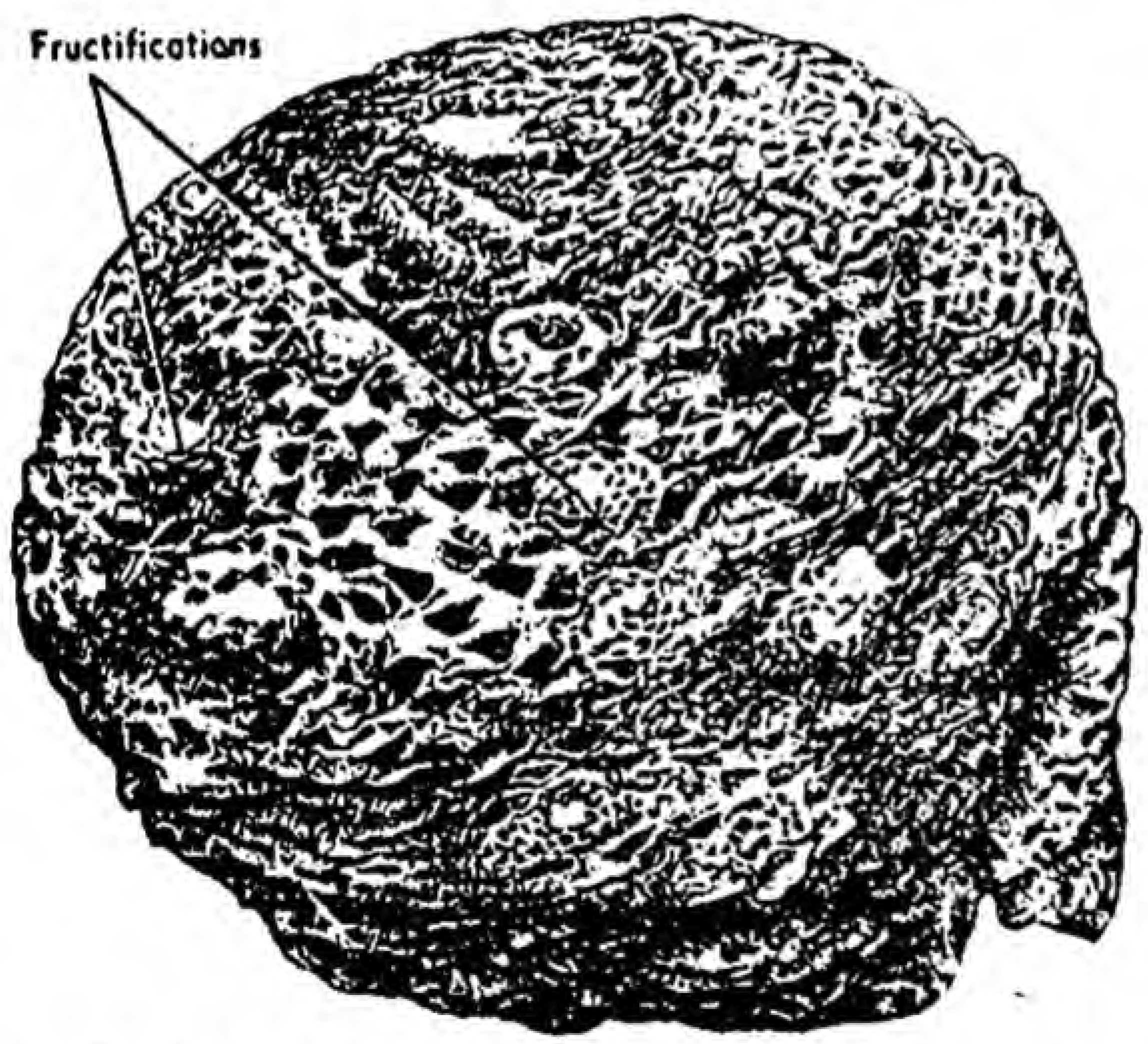



Fig. 3—1 Lateral view of an unbranched trunk of *Cycadeoidea dacotensis* (After Wieland).

The leaves of *Cycadeoidea* were pinnate-compound, nearly three metres long. They were similar to *Macrozamia*, *Encephalartos*, etc.

HISTOLOGICAL FEATURES—The trunk of *Cycadeoidea* possessed centrally situated, large, parenchymatous pith which was surrounded by a thin zone of xylem. The xylem cylinder was

1. Walton, J 1953 : 163.
2. Arnold, C. A. 1961 : 254.

punctuated by radially extending, parenchymatous, medullary rays. The protoxylem was towards the centre (endarch) and the metaxylem was situated towards the cortex. The parenchymatous cortex had mucilage canals and leaf-traces. Epidermis of the stem was not distinct because of the presence of a thick mantle of leaf-bases. In between the leaf-bases a ramentum of flattened scale-like hairs was present.

The leaf-trace was always single at the point of its origin but as it reached the cortex it divided into several mesarch vascular bundles which were arranged in a horse-shoe-shaped manner.

The rachis (=petiole) received the trace supply from a single strand originating from the stem.

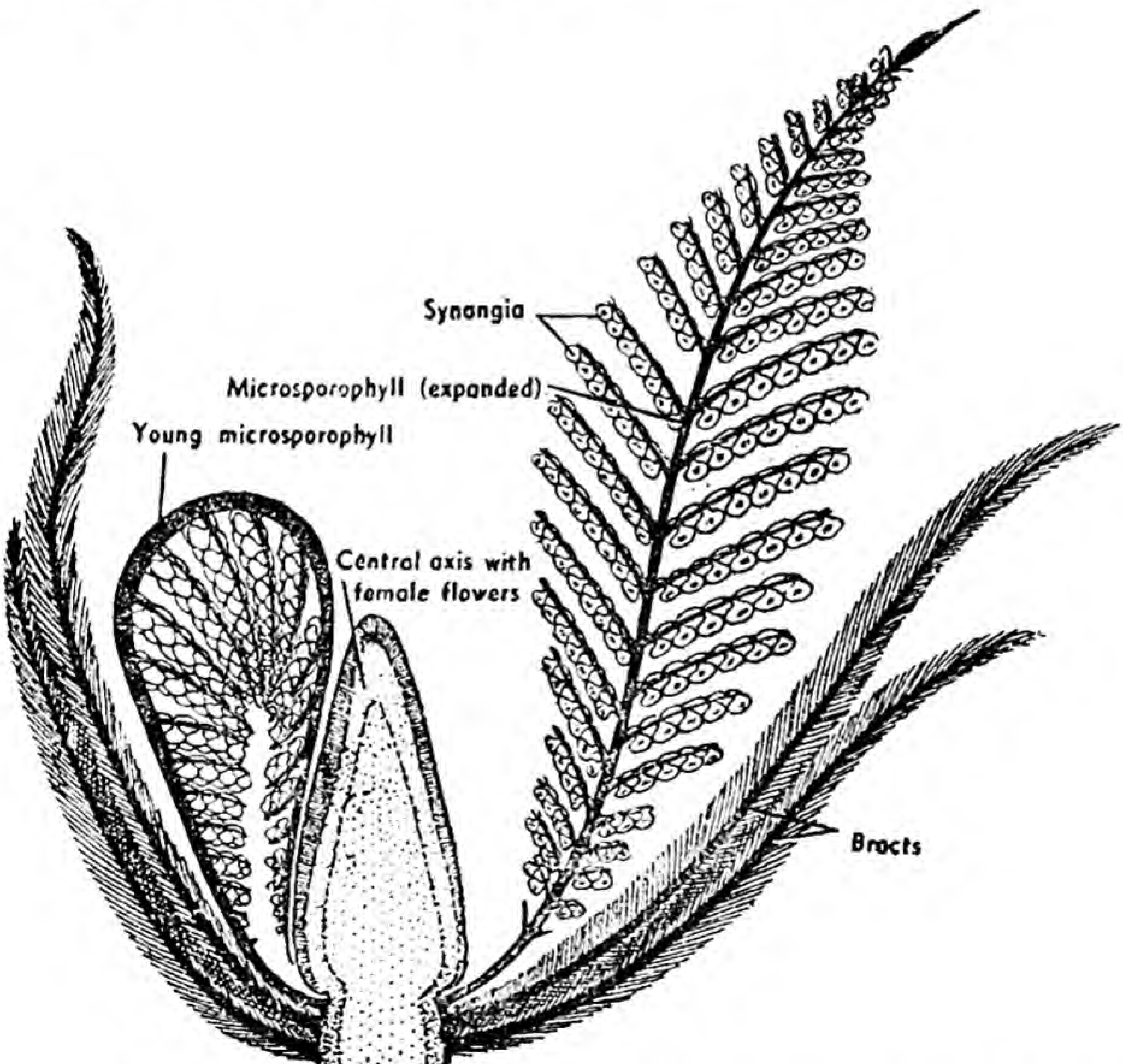



Fig. 3—2 Apical portion of *Cycadeoidea dacotensis* with expanded and curved microsporophylls and a conical central axis possessing female reproductive structures (After Wieland).

**Secondary Growth**—Secondary growth was present in the cycadeoids. Secondary wood consisted of scalariform tracheids and small wood rays. The latter were mostly uniseriate, often biseriate and these extended up to the cambium or even up to the phloem.

REPRODUCTIVE ORGANS - The "flowers" of *Cycadeoidea* were borne on short axillary shoots and were not terminal. In *C. blanca, C. magnifica* and *C. aequalis* the fertile axillary shoot was a stout branch which extended laterally from the main trunk. The fertile shoots possessed a large number of spirally arranged pinnate bracts borne on a central peduncle (fig. 3-3). Delevoryas[1] observed a dense mass of ramental scales on the pinnate bracts. The peduncle was terminated by a conical ovulate receptacle which bore the ovules and interseminal scales (fig. 3-3). In *C. gibsonianus* (=*Bennettites gibsonianus*) the receptacle was convex and cushion-like in shape. In *C. wielandi* the receptacle possessed a cluster of stalked ovules and interseminal scales. The receptacle was elongated and conical in *C. dacotensis* and *C. ingens*. In these two species the seeds had a short-stalk and were situated at right angles to the surface. In *C. dacotensis* the upper two-third portion of the receptacle possessed a large number of spirally arranged hairy bracts and interseminal scales.

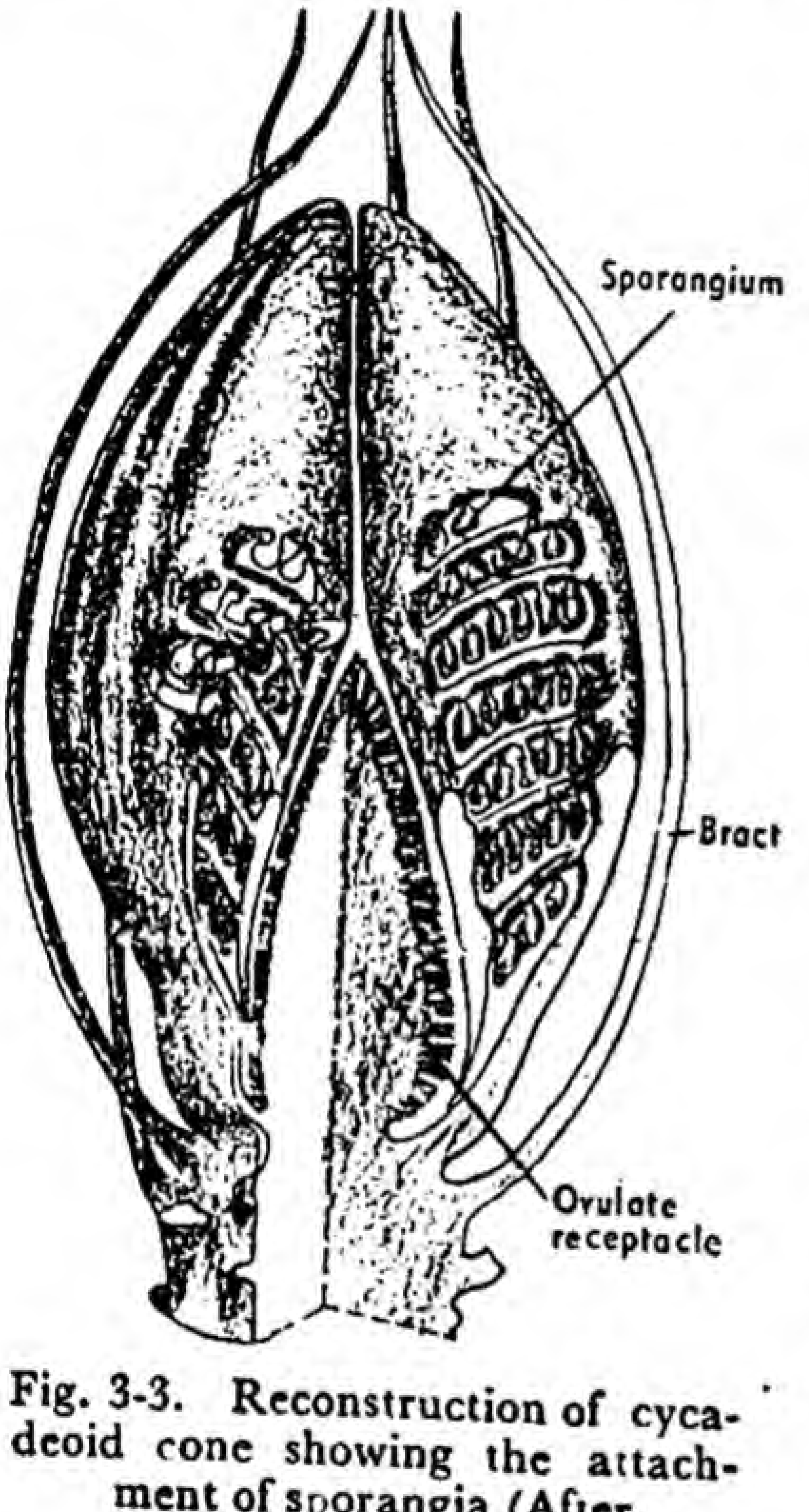



Fig. 3-3. Reconstruction of cycadeoid cone showing the attachment of sporangia (After Delevoryas).

Wieland[1] assumed that the mature bracts of *Cycadeoidea* expanded to form a saucer-shaped perianth which surrounded the androecium (=microsporangiate organs) and the gynoecium

1. Weiland, G. R. 1906.

(=megasporangiate organs) (fig. 3-2). The "flowers of *Cycadeoidea* were small, rosette-like and occurred sporadically among the leaf-bases.

While reinvestigating the morphological nature of the reproductive organs of *Cycadeoidea ingens*, *C. dacotensis* and *C. colossalis*, etc., *Delevoryas*[2] came to the conclusion that the microsporophylls of these plants did not, on maturity, expand into 'flower-like structures' as was postulated by Wieland[1]. Further, he showed that the cycadeoid strobilus had a parenchymatous dome in the centre, which was surrounded by microsporophylls. The tip of the microsporophyll was sometimes fused with the base of the dome. The synangia were borne along the trabeculae, not on the pinnae as was thought by Wieland[1]. These trabeculae connected the outer wall of the androecium with the inner one.

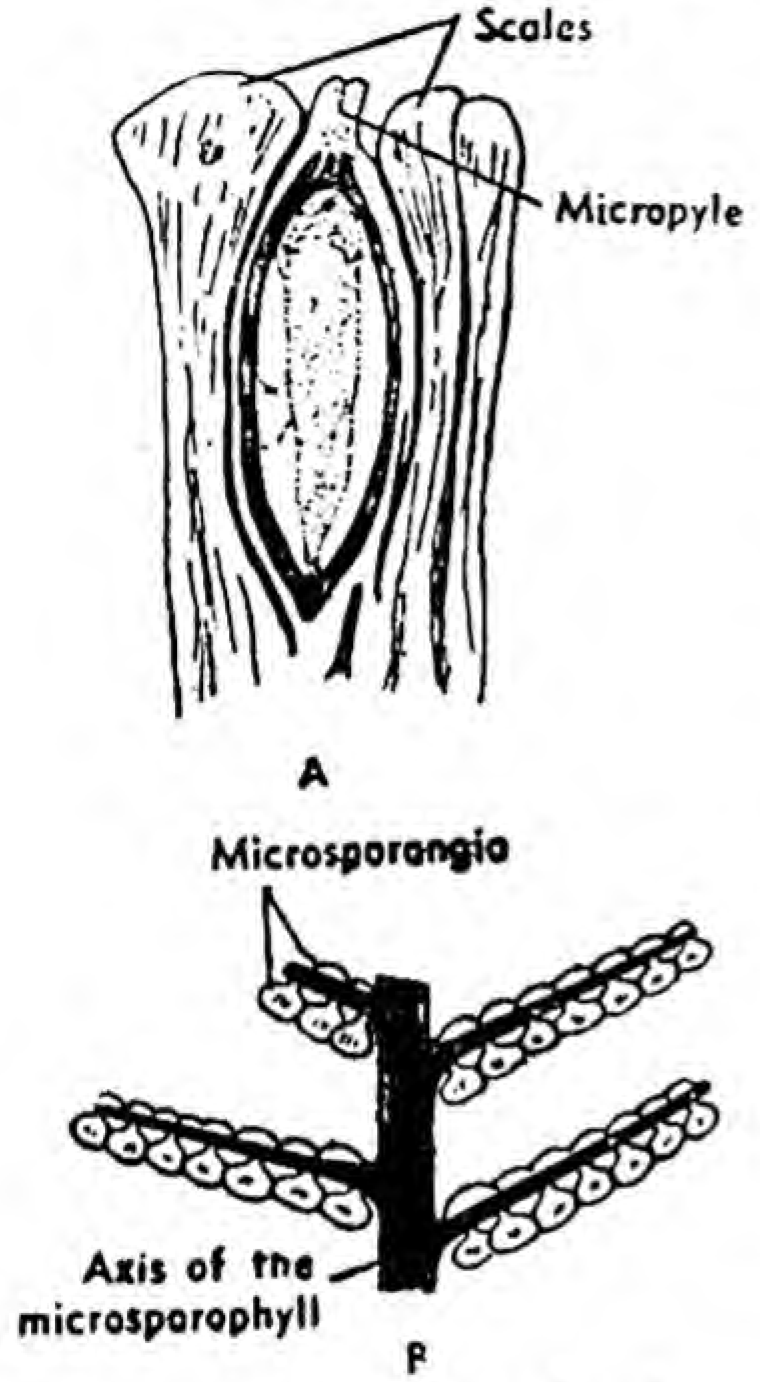



Fig. 3—4 The reproductive structures of *Cycadeoidea dacotensis* (After Wieland). A—L.S. of the seed with micropyle above. The seed is surrounded by scales on either side; B—Portion of a male reproductive organ with pendant microsporangia.

**Male reproductive organs**—The microsporophylls (=stamens) were borne below the ovuliferous receptacle. They were 8-18 in number and arranged in a whorl. The bases of microsporophylls were fused together to form a disc. Each microsporophyll consisted of a main rachis with two rows of trabeculae, each bearing two rows of sac-like 'synangia' (figs. 3-4 & 3-5). In bisporangiate "flowers" the microsporophylls appeared to be incurved with their outer surfaces pressed against the ovulate receptacle. A pair of fleshy appendages have been reported to occur on the dorsal surface in *C. colossalis*.

1 Wieland G R. 1906.
2. Delevoryas, T. 1963.

Each synangium had a short stalk (fig. 3-5A). The synangium was small and pouch-like in appearance. It was shorter in length as compared to its width. The wall of the synangium was made up of palisade-like cells. Each synangium had 20-30 peripheral partitions, each representing a single sporangium. Synangia dehisced by a longitudinal slit into two valves from which a large number of spores were discharged. *C. dacotensis* had nearly unipinnate microsporophylls with numerous synangia on each of them. Each synangium was made up of a single layer of large thick-walled cells, this layer was followed by a zone of parenchymatous cells on its inner side (fig. 3-5). A ring of several microsporangia occurred towards the periphery of the parenchymatous zone.

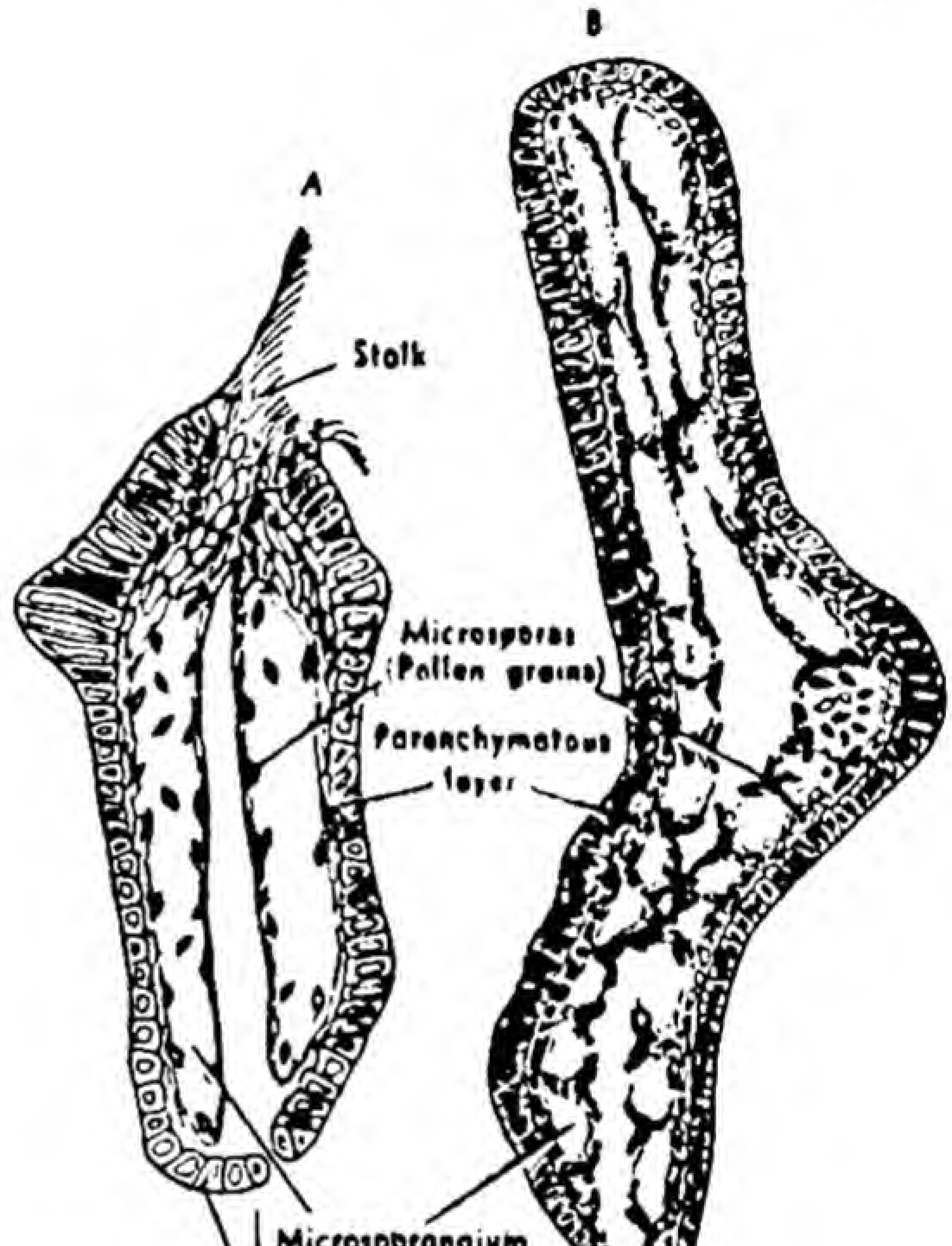



Fig 3—5 Histological details of the structure of a synangium of *Cycad-oidea dacotensis* (After Wieland). A—L S. of the synangium with a stalk and two microsporangia. B—T.S. of the synangium with thickened outer wall and parenchymatous inner layer.

Elaborating the structure of the male reproductive organs Delevoryas[1] states that the sporophyll could be likened to a single wedge of an orange fruit. Now from this wedge, the flesh, from within the wedge is removed and 'windows' or spaces are cut out of the two lateral flat faces of the wedge, leaving oblique strips of membrane intact. These strips extend from the outer

1. Delevoryas, T. 1968.

face of the wedge to the narrow edge. Sporangia are supposed to have been suspended from these bars between the 'windows'. Such a structure according to Delevoryas could be likened to a cycadeoid male reproductive organ.

**Female reproductive organs**—The ovules (=megasporangia) had long stalks and these were arranged in a cone-like fashion on the apex of the fertile shoot which terminated into an ovuliferous receptacle (fig. 3-2). The ovules were orthotropous and they had long micropylar beaks which projected beyond the surface of the ovule-bearing layer. Ovules alternated with interseminal scales, thus their number was the same as that of the ovules. Apically these scales expanded to form a club-shaped structure. The expansion completely occupied the space between two adjacent ovules. The micropyle and the flat expanded part of the scale projected slightly above the general surface (fig. 3-4 A). The ovules were almost completely protected.

In *Benneticarpus crossospermus* Harris, the micropyle was surrounded by a micropylar plate. Harris[1] compared the micropylar plate with adjoining interseminal scales and advocated the view that the interseminal scales were homologous with seeds and were in fact formed by the diverted development of seed initials.

Seeds—The seeds of cycadeoids were quite small in size ; they were oval in shape and measured only a few millimeters in length (fig. 3-4 A). 500 to 600 strobili are reported to have occurred on a single trunk of *C. dartoni* Wieland.

MORPHOLOGICAL NATURE—Wieland[2] was of opinion that the cycadeoids were the "Flowering plants of Mesozoic". He believed that the cycadeoids gave birth to the modern flowering plants. This presumption was based on the belief that the cycadeoid fructifications resembled the magnolian inflorescence in the spiral series of bracts below the stamens (=microsporophylls) being homologous to the calyx and corolla of *Magnolia* There is further resemblance in the presence of numerous stamens ; in the occurrence of a cone-like receptacle ; and in the presence of

1. Harris, T. M. 1932.
2. Wieland, G. R. 1906.

scalariform pitting in the xylem tracheids of both. This theory of derivation of angiosperms from Bennettitalean flower was further elaborated by Oliver & Scott[1] and Arber & Parkin[2].

However, these presumptions did not stand the test of time because the cycadeoid ovule is truly gymnospermous and it has no carpel like that of *Magnolia*. The pericarp of *Cycadeoidea* is formed by the fusion of interseminal scales, it bears no homology with the carpel and the fruit-wall of *Magnolia*. The cycadeoid microsporophylls are pinnate structures, reflecting their filicinean or pteridospermous affinities and they cannot, therefore, be regarded similar to the stamens of *Magnolia*.

## *WILLIAMSONIA* Carruthers

*Williamsonia* occurs mostly as a compression fossil in the Mesozoic. It is similar to the living cycads in several respects. Stamens, ~~leaves as well as~~ fructifications ~~have been studied~~ in detail. *W. gigas* (L & H) Carr., the ~~most studied species was collected from Yorkshire.~~ Its trunk was two metres or more in height. *Bucklandia indica* Seward described from the Rajmahal Hills, Bihar (India), is now considered to be the stem of *Williamsonia sewardiana*[3]. It occasionally possessed unequal branches.

MORPHOLOGICAL FEATURES—*Williamsonia sewardiana* Sahni, collected from the Rajmahal Hills, Bihar, was a small tree with a columnar trunk, measuring more than 2 metres in height. At its apex was present a crown of leaves somewhat like that of the cycads[4]. The leaves of *Williamsonia* were pinnate-compound and are named *Ptilophyllum cutchense* McCl. The trunk possessed two kinds of leaves (i) long pointed and scale-like, which left small scars and (ii) parallel-veined foliage leaves, these left large scars. Leaf-bases were persistent, they formed a thick armour round the trunk as in the living-cycads. (fig. 3-6)

HISTOLOGICAL FEATURES—The trunk of *Williamsonia sewardiana* Sahni (=*Bucklandia indica* Seward) possessed a small

1. Oliver F. W. & D. H. Scott 1906.
2. Arber E.A.M. & Parkin 1907.
3. Sitholey, R. V. 1963.
4. Sahni, B. 1932.

centrally situated pith, measuring nearly 1 cm. It was surrounded by a ring of xylem and had radially extending medullary rays. Xylem was endarch, i. e., protoxylem pointed towards pith and metaxylem away from it. Pith and cortex both were parenchymatous and they contained irregularly-distributed secretory sacs.

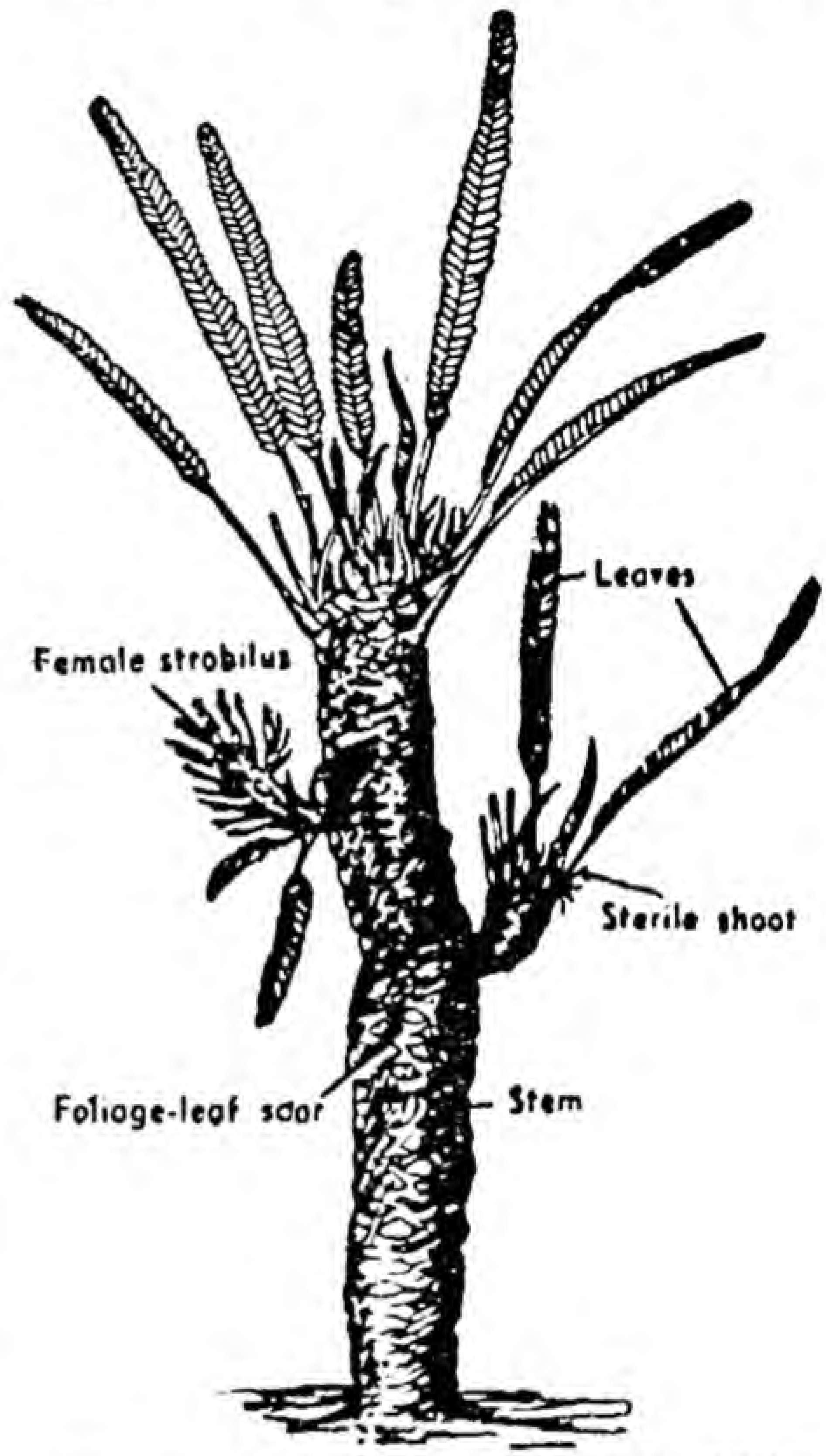



Fig. 3—6 Reconstruction of *Williamsonia sewardiana* Sahni with a female strobilus (in sectional view) and a sterile shoot (After Sahni).

Secondary growth was extensive and the secondary wood was compact unlike that of the cycads, xylem tracheids had multiseriate bordered pits. This type of secondary wood resembles the wood that occurs in conifers. Wood rays, mostly uniseriate, were numerous, sometimes they were bi- or triseriate and extended up to the cambium or the phloem.

REPRODUCTIVE ORGANS—The fructifications of *Williamsonia* were borne on lateral branches. Some of these were sterile as they bore foliage leaves, bracts and scales only; others were fertile. Bracts occurring on the lower region of lateral shoots were simple like those on the trunk but those that occurred towards the apex were pinnate-compound, they served as bud scales. Male and female fructifications were borne on separate plants; the "flowers" thus were unisexual and the plants dioecious.

**Male reproductive organs**—The male reproductive organs of *Williamsonia sewardiana* Sahni have not yet been found. Staminate (=microsporangiate) 'flower' of *W. spectabilis* Nathorst is, how-

ever, known. It was nearly 9 cm in diameter and was enclosed by a basal cup formed by fused stamens (=microsporophylls). The basal cup itself measured nearly 3 cm in diameter. Microsporangia were borne in the form of synangia on the lateral pinnae.

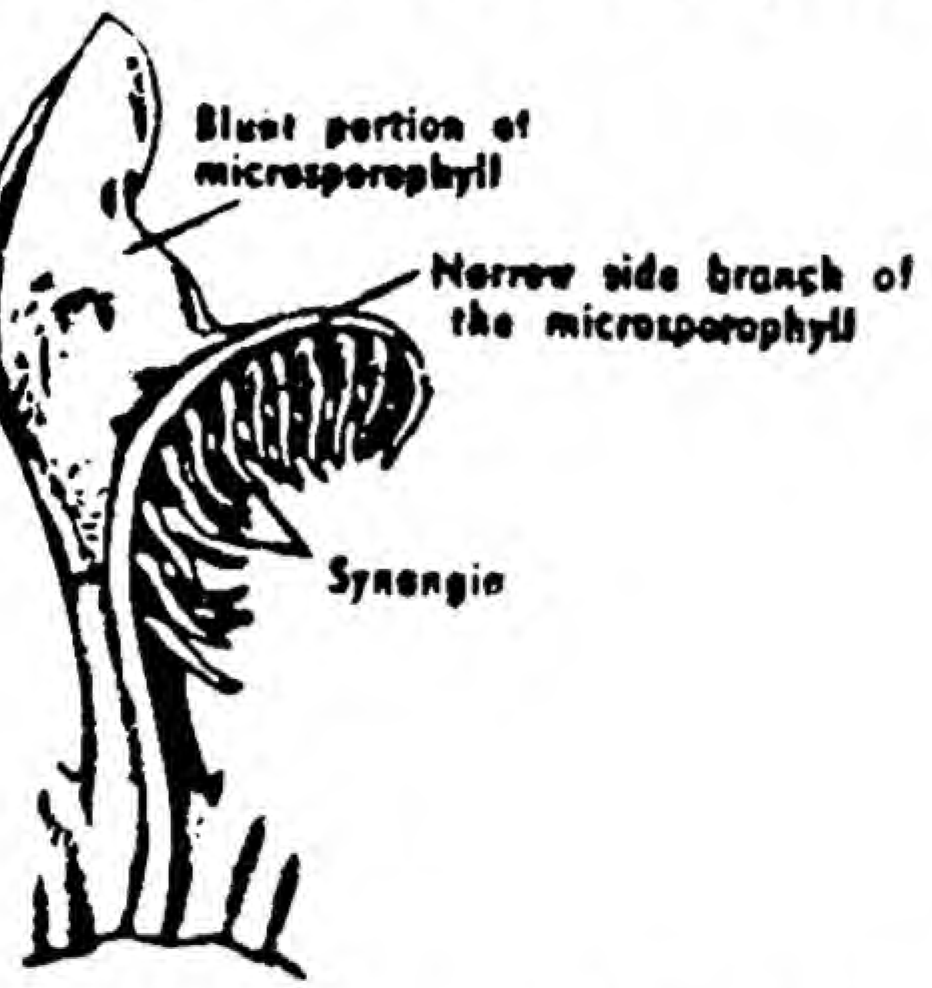



Fig. 3—7 Reconstruction of microsporophyll of *Williamsonia santalensis* with blunt apex and narrow side branch and synangia attached to it (After Sitholey & Bose).

An incomplete specimen of male fructification from the Rajmahal Hills, Bihar, *W. santalensis* has been described by Sitholey and Bose.[1] It possessed a shallow basal cup. The microsporophylls were attached to the cup; they were divided into two parts, a blunt terminal portion and a narrow side branch. The latter possessed two rows of finger-like synangia (fig. 3-7 . Two more species of *Williamsonia*, namely *W. setosa* Nathorst and *W. sahni* Gupta with microsporangiate structures have been found in the Rajmahal Hills, Bihar.

**Female reproductive organs**—The female reproductive organs or ovules of *Williamsonia sewardiana* were borne on a central receptacle which was constituted by stalked ovules mixed with interseminal scales (fig. 3-6). The ovule had an elongated nucellar region and distally-extended apical funnel (=micropylar beak). The entire female fructification was enclosed by several long bracts. The bracts had scales at the base and hairy ramenta above.

Another female fructification, *W. scotica* had closely packed ovules and interseminal scales. The ovule had a short stalk and the nucellus was covered by a single envelope which extended up to the micropylar beak. Some other female fructifications referred to this genus are *W. mexicana* and *W. whitbiensis* Nathorst

1. Sitholey, R. V. & M. N. Bose 1953.

## *WILLIAMSONIELLA* Thomas

*Williamsoniella* is a genus which is placed in the family Wielandiellaceae. It was more profusely branched than *Williamsonia*.

MORPHOLOGICAL FEATURES—*W. coronata* Thomas, the most studied species of this genus, possessed dichotomously branched trunk. The foliage of *Williamsoniella* is known as *Nilssoniopteris vittata* [= *Taeniopteris vittata* (Brong.)] Florin. The leaves were linear with a thick midrib and broad lamina which had many closely packed lateral veins (fig. 3-8).


Fig. 3—8 Reconstruction of *Williamsoniella coronata* with branched stem and leaves. Strobili situated in the dichotomies (After Thomas).

REPRODUCTIVE ORGANS—The fructifications of *Williamsoniella* were borne upright in the angles of the dichotomies. They were bisexual and smaller than those of *Williamsonia*. Basal bracts were absent. The peduncle of the fructifications (= flowers) measured 3.5 cm in length (fig. 3-8).

**Male reproductive organs**—Microsporophylls (=stamens) were fleshy and 12 or more in number, these were borne below the female reproductive organs. Each microsporophyll was like the segment of an orange in appearance (fig. 3-9). It had finger-like branches in the central region which partially enclosed two pairs of 'capsules' (= synangia). Thus there were four synangia on each microsporophyll. Each capsule had a large number of spores. Below the microsporophylls were hairy-bracts which were perianth like.

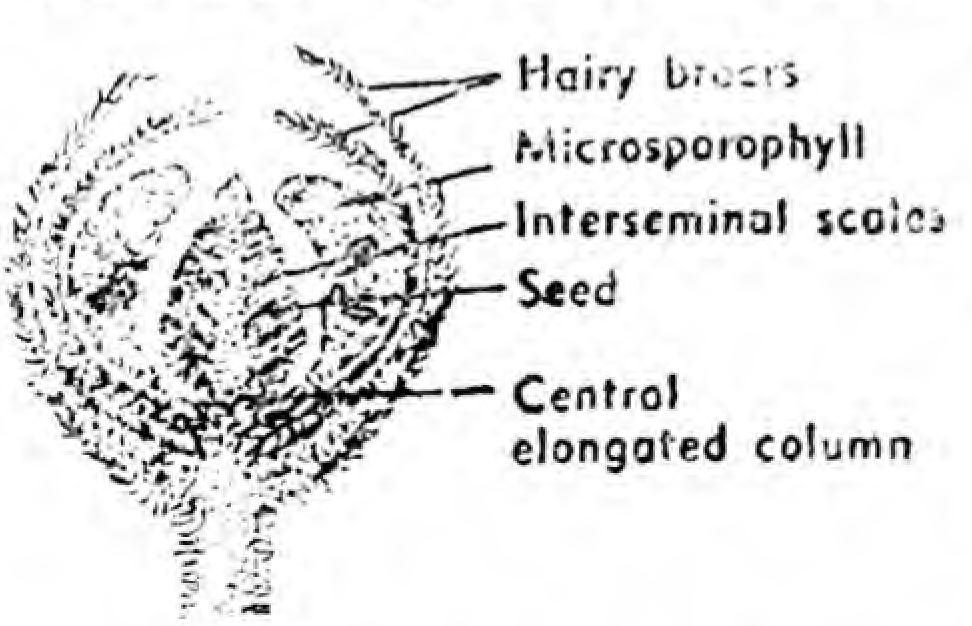



Fig 3—9 V. S. of the reproductive organs of *Williamsoniella coronata* (After Harris).

**Female reproductive organs**—The ovules in *Williamsoniella* were sessile and were directly attached to the sides of the receptacle between numerous interseminal scales which ended into knob-like structures.

## *WIELANDIELLA* Nathorst

*Wielandiella* is another fossil cycadophyte that occurred in the Mesozoic. It belongs to the family Wielandiellaceae.

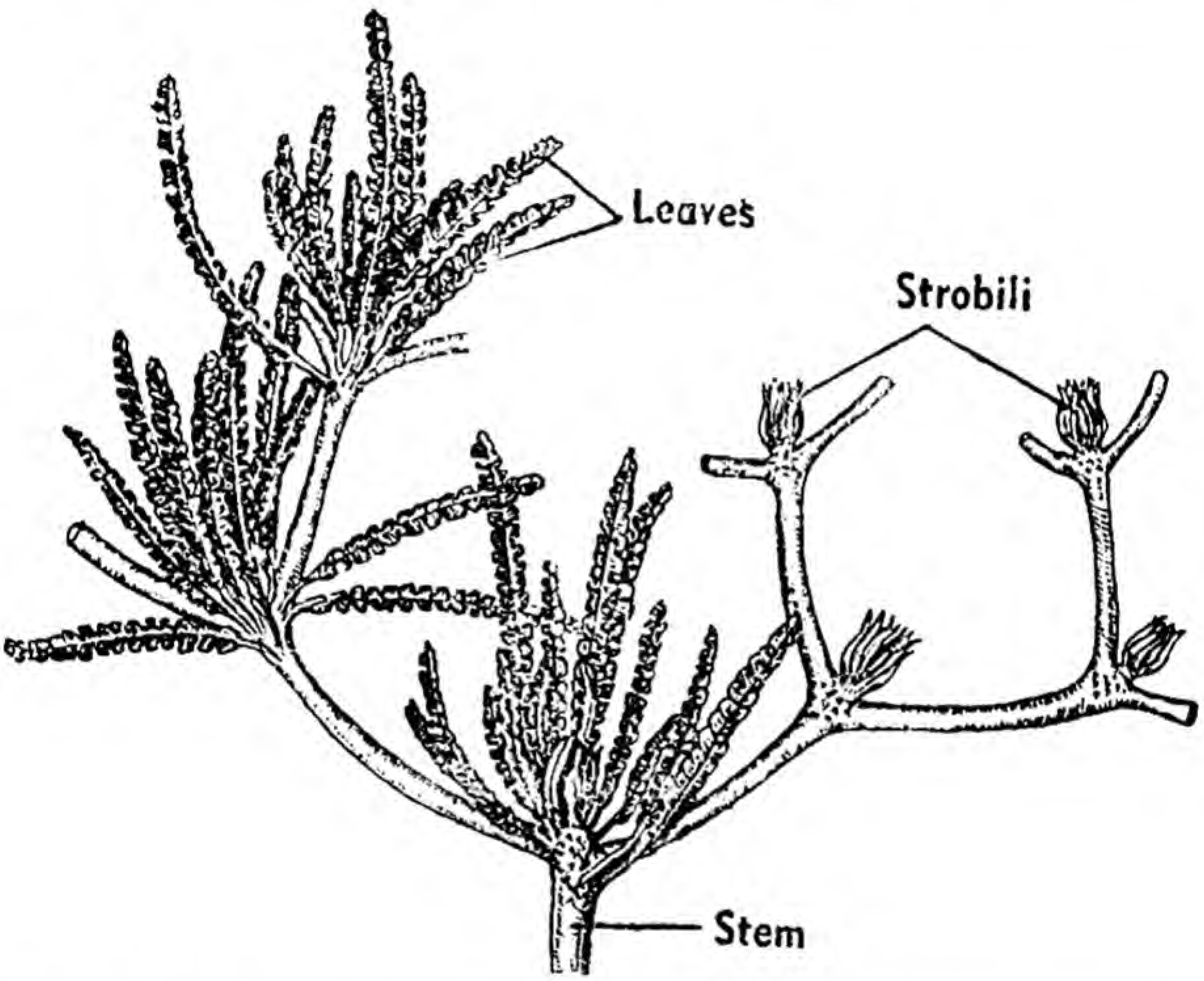



Fig. 3—10. Reconstruction of *Wielandiella angustifolia* with clusters of leaves and strobili situated at the dichotomies (After Nathorst).

*W. angustifolia* Nath., the only well-known species of this genus, was collected from Sweden. It resembled *Williamsoniella* in its dichotomous mode of branching. The trunk measured about 1.5 cm in diameter and showed false dichotomy. Leaves nearly 8 cm in length were pinnate-compound and they are known as *Anomozamites minor*. They were borne in clusters at the dichotomies of branches (fig. 3-10). The fructifications of *Wielandiella* were probably bisexual.

**AFFINITIES OF THE CYCADEOIDALES**—The cycadeoids in many respects resemble the ferns and cycads, yet in other characters they differed from them and hence form a distinct group of gymnosperms.

**Resemblances with ferns**—The cycadeoids resemble ferns in the presence of a crown of leaves, persistent leaf-bases, mesarch nature of vascular bundles, direct course of leaf-traces through the cortex and many other characters. Cycadeoids also resemble the Marattiaceous ferns in the structure of their synangia.

**Resemblances with cycads**—There is similarity between the habit of cycadeoids and cycads. Secondly the seeds in these two groups resemble each other especially with *cycas* in being dicotyledonous. They are however very much smaller; consequently, therefore, they were probably exendospermic. In having bisporangiate reproductive organs cycadeoids differ markedly from cycads.

## Chapter 4

# Cycadales

GENERAL CHARACTERS—The different genera belonging to the order Cycadales[1] are popularly called the 'Cycads'. The order includes three families viz., Cycadaceae Stangeriaceae and Zamiaceae with ten genera and about 77 species, which are predominantly distributed in warmer parts of the globe. The cycads have been considered to be of great botanical interest because they possess several primitive characters which are absent in other gymnosperms. They bear affinities with ferns on the one hand in such characters as the arrangement and vernation of leaves (fig. 4-9) and motile nature of male gametes (fig. 4-37D) and on the other hand, they resemble the pteridosperms, a group of fossil gymnosperms, which does not exist now, in having thick cortex, large pith, centripetal metaxylem, pinnate leaves and the structure of the ovule.

The mesozoic era is called the 'Age of the Cycads', as they were abundant and widespread at that time, though the cycads appeared first in the Triassic. The other group of gymnosperms which was contemporaneous with the cycads was the Cycadeoidales (=Bennettitales).

DISTINGUISHING FEATURES—In general, most of the living cycads are xerophytes. Their growth is slow and branching rare. Among the living cycads, *Macrozamia hopei* T. Hill ex C. Moore is the tallest and *Zamia pygmaea* Sims. the smallest cycad. Some of them possess columnar trunks. The cycads have the following distinguishing features:

They are long lived and resemble palms or tree ferns in their habit. Gymnosperms and ferns both have unbranched stem and

1. Coulter, J. M. & C. J. Chamberlain 1910.

large pinnate leaves which form a crown (fig. 4-11). The trunk is either long and columnar, e.g., *Dioon*, *Microcycas*, *Macrozamia*, *Encephalartos*, or short and stumpy, e.g., *Bowenia*, *Stangeria*, *Zamia*, etc. It possesses armour of persistent leaf and sporophyll-bases (fig. 4-12). Two kinds of leaves are present viz., foliage leaves and scale leaves. Foliage leaves assume different dimensions in different plants. They are mostly unipinnate, rarely they may be bipinnate, as in *Bowenia*. Lamina is linear, sometimes ovate, entire or serrate. Geotropic as well as apogeotropic or coralloid roots may be present (fig.4-14). They are usually di- to tetrarch. Vascular bundles are radial and the xylem is exarch (fig. 4-15). Stem in young stage is monoxylic (fig. 4-17) possessing conjoint, collateral and endarch vascular bundles. Activity of primary cambium is meagre. Anomalous secondary growth takes place by the formation of successive rings of cambia (fig. 4-22). Wood is manoxylic, mucilage canals may be present in pith and the cortex. Leaf traces are pseudomesarch or diploxylic in the living genera. Vascular bundles of pinnae are also pseudomesarch with well developed transfusion tissue (fig. 4-25A&B). Stomata are sunken and haplocheilic (fig. 4-26). Plants are dioecious, microsporophylls are scale-like or peltate and they are arranged in the form of strobili (fig. 4-32), but the megasporophylls are loosely arranged in *Cycas* (fig. 4-28). Strobili are either terminal or lateral. Microsporangia develop in sori on abaxial (lower) surface of the microsporophylls (fig. 4-34) and the megasporangia which are few in number arise laterally on either side of the megasporophylls (fig. 4-29&4-30). The megasporophylls are foliar in *Cycas* and are covered with hairs or ramenta (fig. 4-29). The tips of megasporophylls are sterile. Megasporangia (ovules) are orthotropous, they possess a three-layered envelope, a pollen chamber and micropylar canal, etc. (fig. 4-31). Microspores (pollen grains) are liberated at three-celled stage, their maturation takes place in the pollen chamber of the ovule (fig. 4-36H). Pollination is anemophilous. Male gametes are multiflagellate and motile. They show flagellar as well as amoeboid movements. Pollen tube is haustorial in nature (fig. 4-37). Archegonia are 2 or more in number with usually two neck cells (fig. 4-36). Neck canal cells are absent and the ventral canal cell is represented uane uyclqs

and there is no wall separating the ventral canal nucleus from the egg. Endosperm develops from the tissue of the female gametophyte before fertilization. Fertilization is siphonogamous accompanied with zooidogamy. Proembryo and suspensor are formed during the development of the embryo. Cotyledons are usually two (fig. 4-39), rarely 1 or 3. Seeds are large and their germination is epigeal. Shrivelled cotyledons remain attached to seedling for pretty long time.

GEOGRAPHICAL DISTRIBUTION—The Cycadales includes ten genera. Among these, *Dioon, Ceratozamia, Microcycas* and *Zamia* occur in the Western Hemisphere hence they are called the Western cycads, while, *Cycas, Encephalartos, Stangeria, Macrozamia, Bowenia* and *Lepidozamia* are distributed in the Eastern Hemisphere, they are, therefore, called the Eastern cycads.

**Distinguishing features of the Cycadales**—There are three families: Cycadaceae, consisting of the genus *Cycas;* Stangeriaceae with one genus *Stangeria*; and Zamiaceae which includes the remaining eight genera. They are characterized by nervation of the leaflets[1].

**Cycadaceae**—midrib with no lateral nerves.
**Stangeriaceae**—midrib with lateral veins.
**Zamiaceae** — numerous longitudinally running nerves parallel or wavy, simple or forked.

The different genera of the order Cycadales possess the following distinguishing characters:

*Cycas* Linn.—Leaves unipinnate, leaflets with a single midvein without lateral veins; megasporophylls foliar with 2 to 10 ovules (fig. 4-1). Johnson[2] states that there are 20 species in all.


Fig. 4—1 *Cycas circinnalis* with megasporophylls and a crown of foliage leaves (After Blume)

1. Johnson L.A.S. 1959.
2. Johnson, L. A. S. (in J. C. Willis 1966).

*Stangeria* T. Moore—Leaves unipinnate, leaflets with a single midrib and bifurcating lateral veins. Sporophylls aggregated, forming compact strobili. Megasporophylls peltate, each possessing only 2 ovules (fig.4-2).

Fig. 4—2 *Stangeria paradoxa* with tuberous stem and pinnate leaves (After Schuster)

*Dioon* Lindl.—Leaves unipinnate, leaflets parallel veined, veins furcate; medullary bundles absent; megasporophylls loosely compacted (fig. 4-3) in female strobili.

*Macrozamia* Miq.—Leaves unipinnate, leaflets parallel veined, veins furcate; medullary bundles present; sporophylls end in a long spine.

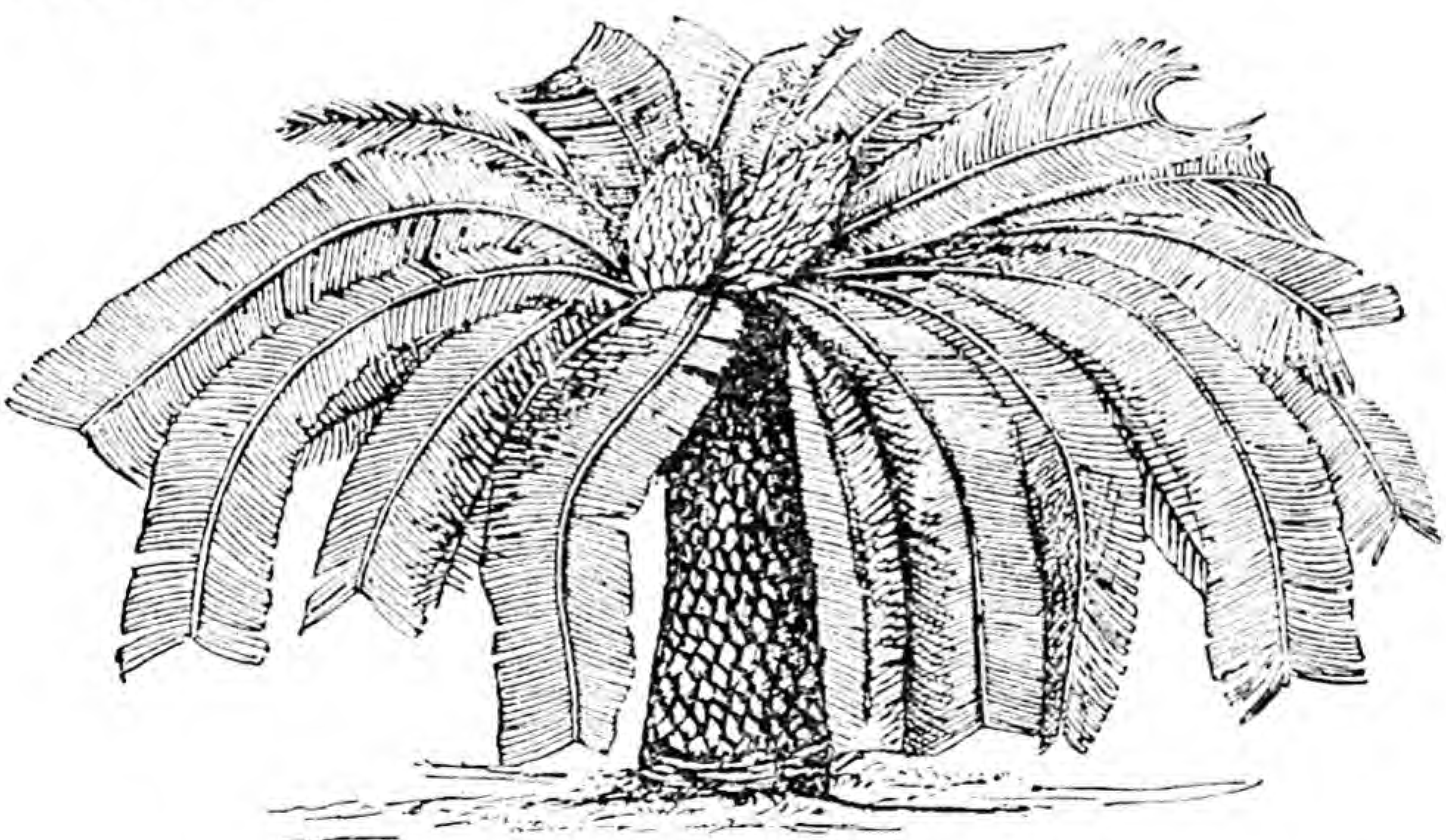


Fig. 4—3 *Dioon edule* (After Schuster)

*Encephalartos* Lehm.—Leaves unipinnate, leaflets parallel-veined, veins furcate; stem polyxylic, medullary bundles present, sporophylls peltate (fig. 4-4)

*Ceratozamia* Brongn.—Leaves unipinnate with a pair of teeth-like stipules. Sporophylls possess two horns.

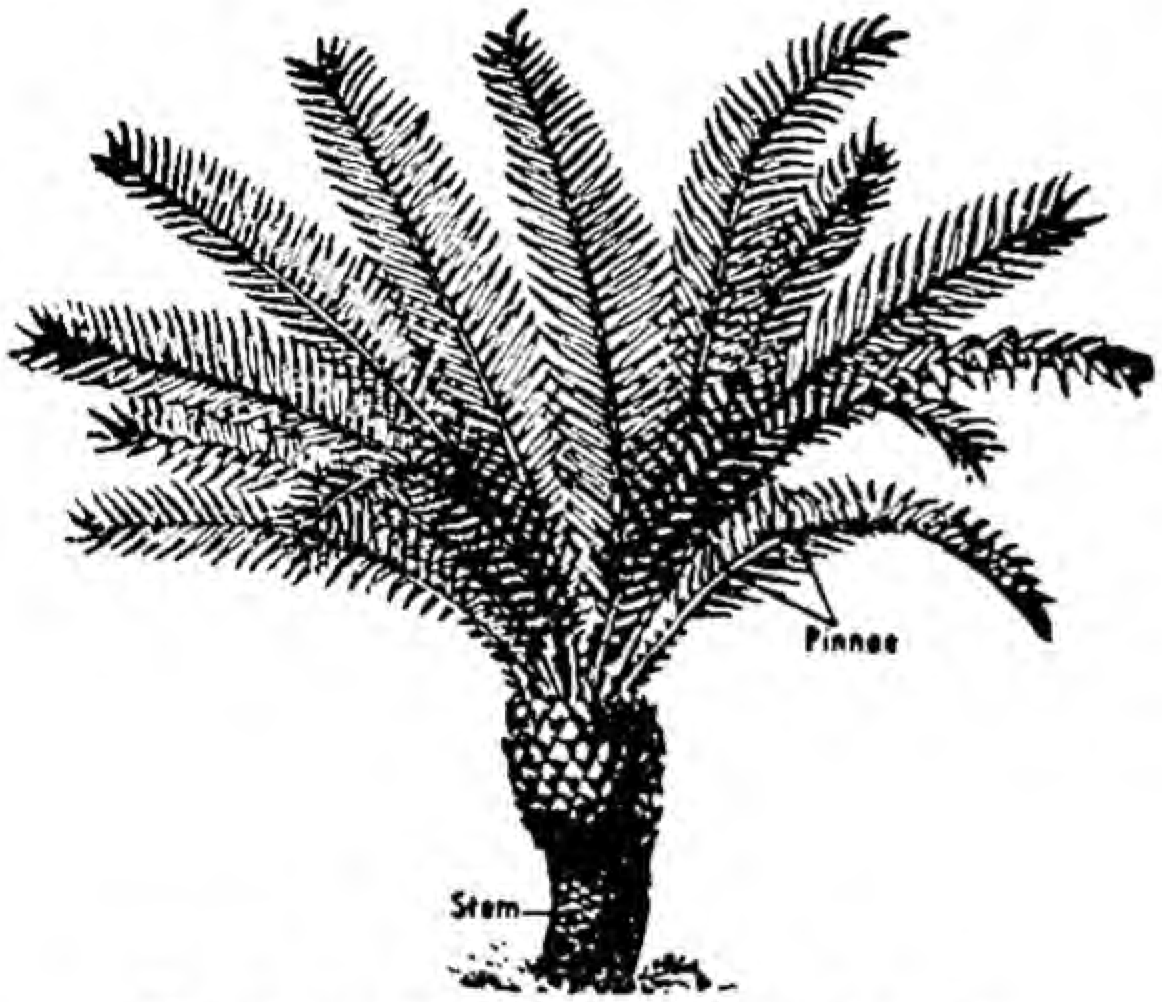



Fig. 4—4 Apical part of *Encephalartos hildebrandtii* with a crown of leaves (After Engler and Prantl)

*Microcycas* A.DC.—Leaves unipinnate without stipules; microsporophylls flat at the apex and megasporophylls peltate; trunk columnar (fig. 4-5).

*Zamia* Linn.—Trunk geophilous; leaves unipinnate with branched lateral veins. Both microsporophylls and megasporophylls peltate (fig. -46).

Fig.4 5.— *Microcycas calcoma* (After Schus ter

*Bowenia* Hook.—Leaves bipinnate compound ( fig. 4-7 ).

*Lepidozamia*[1] Regel.-Trunk 2 to 20 meters tall. Leaves numerous; sporophyll ends acute or bluntly pointed or with a terminal spine. Strobili sessile or subsessile. Successive crowns of fronds markedly separated by broad series of cataphylls. Pinnae with a single thick midrib and no lateral veins. Megasporophylls spirally arranged and falling separately at maturity. Only two living species, *L. peroffskyana* Regel and *L. hopei* Regel are known, from E. Australia.

1. Johnson, L. A. S. 1959

Fig. 4—6 *Zamia integrifolia* with subterranean stem and a megastrobilus at the apex (After Jacquine)


Fig. 4—7 *Bowenia spectabilis* with tuberous stem and bipinnate compound leaves (After Engler and Prantl)

## *CYCAS* Linn.

SYSTEMATIC POSITION—

Order—*Cycadales*
Family—*Cycadaceae*
Genus—*Cycas* Linn.

GEOGRAPHICAL DISTRIBUTION—*Cycas* is the most widely distributed genus of the Cycadales. Its species are distributed from the southern part of Japan to Australia including India, China and the Eastern coast of Africa. In India, *Cycas* is represented by the following six species[1] which may be identified by the characters enumerated below :

Margins of leaflets flat

Trunk not swollen at the base

Leaflets 5 mm. to 10 mm. broad, blade of carpophyll* broadly orbicular, long, acuminate and deeply pectinate.

*1. C. pectinata* Griff.

---

1. Raizada, M. B. & K. C. Sahni 1960.

* Carpophyll=Megasporophyll.

Leaflets usually not more than 12 mm. broad, carpophylls spinous, toothed along the margin.

2. *C. circinnalis*† Linn.

Leaflets 12 mm. to 16 mm. broad, blade of carpophyll ovate to ovate-lanceolate, densely villous, teeth small.

3. *C. rumphii* Miq.

Trunk conspicuously swollen at the base

Leaflets not more than 8 mm. broad, carpophylls pectinate along the margin, blade of carpophyll ovate.

4. *C. siamensis* Miq.

Margins of leaflets revolute

Small palm-like tree, blade of carpophyll pectinate.

5. *C. revoluta* Thunb.

Small shrubs, stem about 15 cm. high, blade of carpophyll dentate-lobate.

6. *C. beddomei* Dyer.

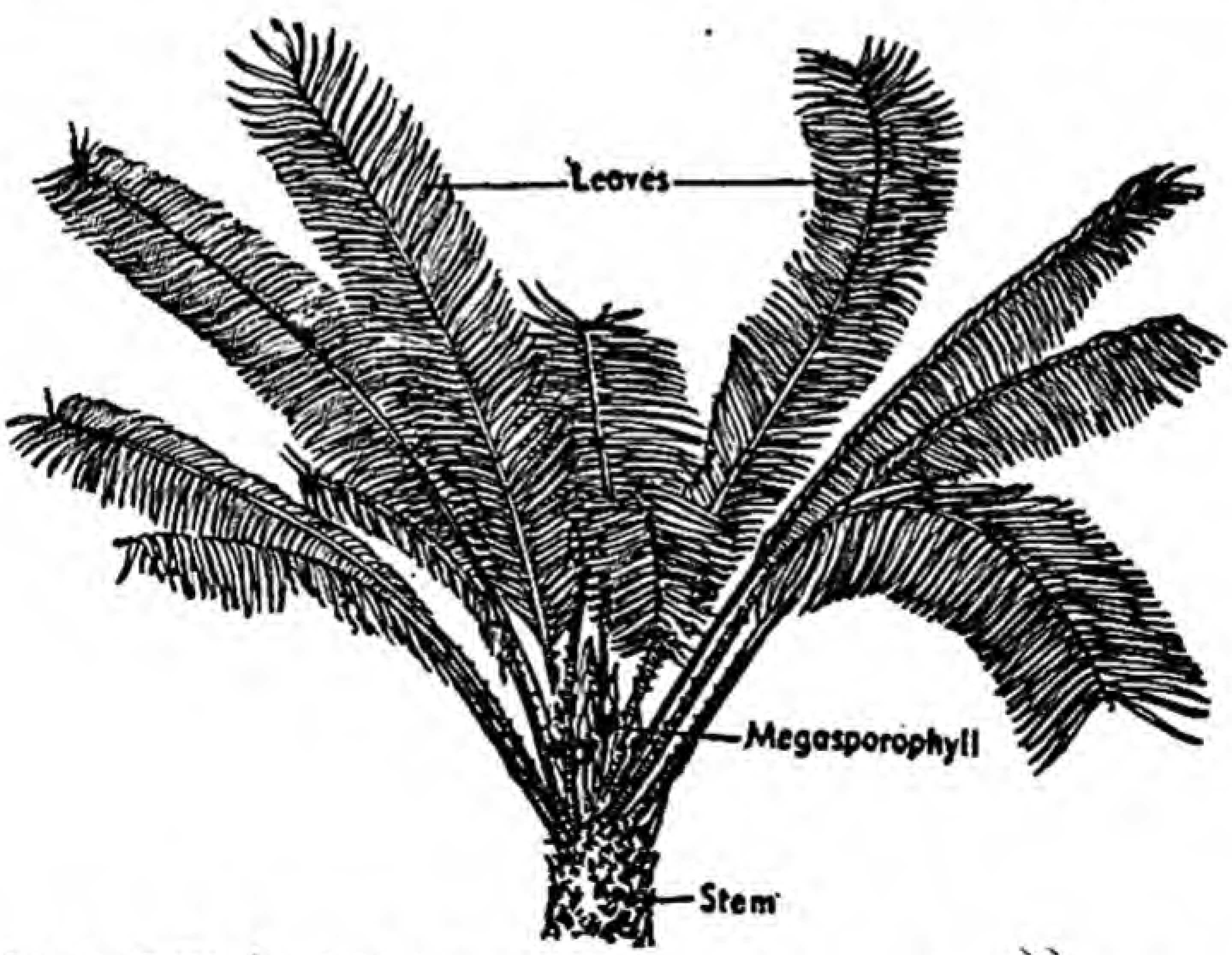



Fig. 4—8 The apical crown of a young plant of *Cycas circinnalis*.

OCCURRENCE AND DISTINGUISHING FEATURES OF INDIAN SPECIES—*Cycas pectinata* occurs in eastern Nepal, Champaran District (Bihar), Sikkim, Assam and East Bengal. In Nepal it is locally called 'Thakal' and in Assam 'Thaljimura'. The

†Spelling after Schuster 1932 : 66.

plants of this species possess thick columnar trunk nearly 1.5 to 2.5 metres high. Megasporophylls are deeply pectinate and bear 4 to 6 ovules.

*C. siamensis* occurs in Burma and is geophilous; stem sometimes up to 2 metres tall. Megasporophyll usually bears two ovules, one on either side of it. Burkill[1] believes that this as well as *C. pectinata* are one and the same.

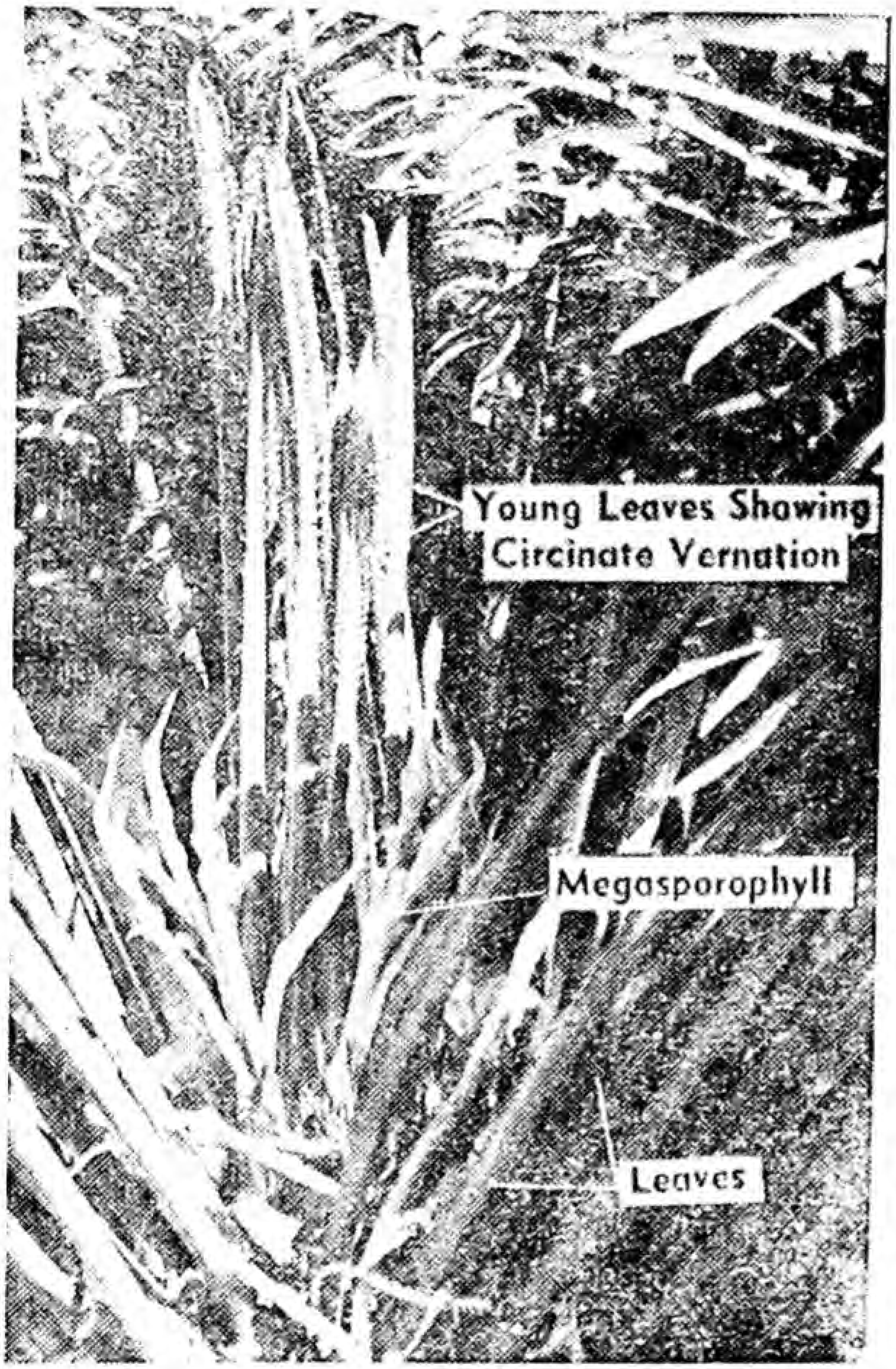


Fig. 4—9 Young leaves aud megasporophylls of *Cycas circinnalis*

*C. circinnalis* occurs in Orissa, Andhra and Madras States and extends to Ceylon, Java, Sumatra, Formosa and Philippines. It bears unipinnate leaves which are 1.5 to 3.0 metres long, with 80 to 100 pairs of leaflets. Megasporophylls are rhomboid in form. They are much longer than broad and have sharp teeth (fig. 4·9). A variety named *C. circinnalis* Linn. var *orixensis* occurs in the hill forests of the Malls of Puri[2].

*C. rumphii* occurs in Burma, Andaman and Nicobar Islands, Celebes, New Guinea, etc. It is usually cultivated in the gardens. It possesses unipinnate leaves 1 to 2 metres long with 50 to 60 pairs of leaflets. Megasporophylls are long, lanceolate and dentate. Sometimes it is difficult to distinguish this species from *C. circinnalis*.

1. Burkill [in Bor. N. L 1953:8].
2. Raizada, M. B. & K. C. Sahni 1960.

*C. beddomei* occurs in Cuddapah, Calicut, etc. It is a dwarf-stemmed species occurring in the hills of Madras. In Tamil, it is called 'Per ita'. The plants are shrub-like in habit, the stem is a few centimetres in height, leaflets are narrow, 2 to 4 mm. broad with revolute margins.

*C. revoluta* occurs in China and Japan. It is widely cultivated in the gardens of our country. As it yields 'sago' it is popularly called 'sago palm'. These plants are palm-like in form, nearly two metres high. Leaflets are 6 to 8 mm. broad with revolute margins (fig.4-10).

Fig. 4—10 Plants of *Cycas revoluta* growing on a hill slope (After McLean and Cook)

According to Pant and Mehra[1] 17 species of *Cycas* are said to occur in the Eastern Hemisphere. L.A.S. Johnson believes that there are 20 species.[2]

~~MORPHOLOGICAL FEATURES~~—*Cycas* is a slow growing, long-lived tropical plant resembling a palm tree in external appearance. The stem is unbranched, erect and stout. When young the stem is tuberous. Swamy[3] reported dichotomous branching of stem in a plant from Mysore. At the apex of the stem occurs a crown of spirally arranged, pinnate leaves which may be 90 to 270 cm. long, in different species

کھجور کا درخت

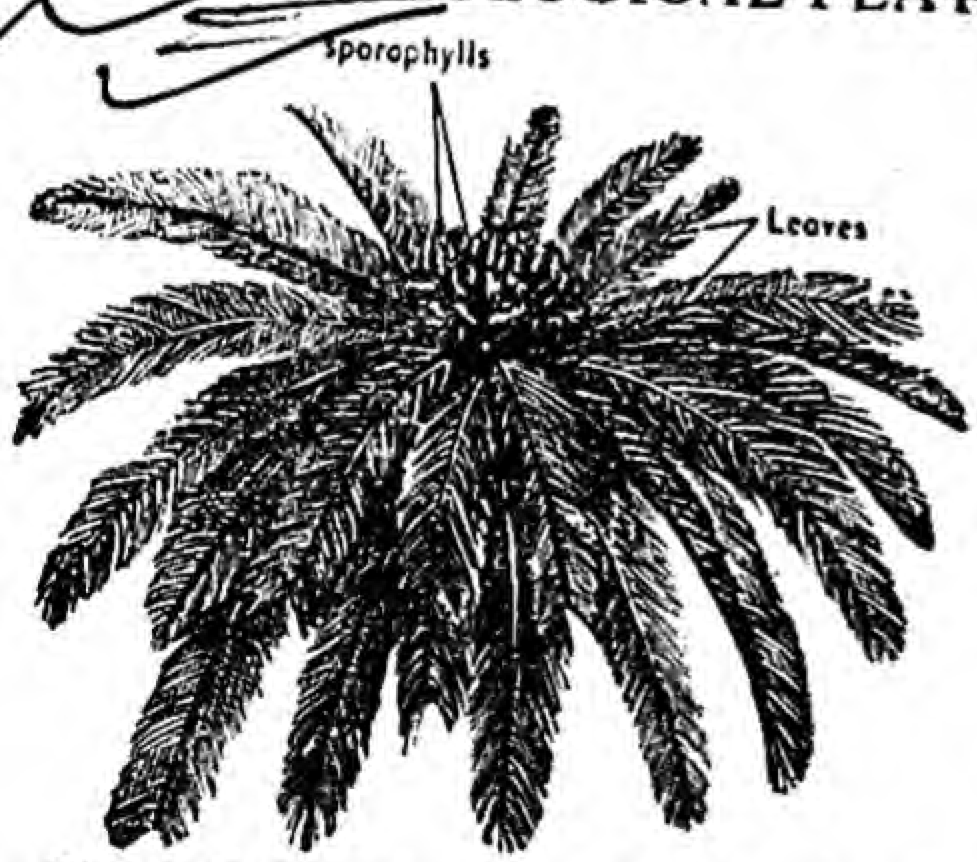



Fig. 4-11 Crown of *Cycas revoluta* showing the arrangement of leaves and megasporophylls (After Wettstein)

1. Pant, D. D. & B. Mehra 1962.
2. Johnson, L. A. S. (in J. C. Willis 1966)
3. Swamy, B. G. L. 1948.

(fig. 4-11). Pinnae are hard and leathery and they are closely set on the rachis. They are sessile with a narrow base and decurrent margins. Lamina may be entire or dichotomised as in *C. micholitzii* Dyer. There also occur small, dry, brown scales alternating with green foliage leaves. Usually a single crown of leaves appears every year. But Pant[1] has reported the formation of two crowns in a year in *C. circinnalis* and *C. rumphii* (in Allahabad), one of which comes up in spring and the other in the monsoon season. According to Coulter and Chamberlain[2] a single crown of leaves persists for more than a year but Pant[3] has reported the occurrence of 4 to 5 crowns, one below the other. The number of leaves borne at the apex increases with the age of the plant. There is no regular leaf fall in *Cycas*, but when the leaves grow old, they bend down and gradually decay. The old stem is sheathed with a hard armour of woody leaf and sporophyll-bases, which persist for several years (fig. 4-12). The leaf-bases provide a rough estimate of the age of the plant. The pinnae have an entire margin, a distinct midrib, but no lateral veins. The leaflets are opposite or sub-opposite to each other and are replaced by spines at the lower end of the rachis in *C. revoluta* and *C. circinnalis*. Scale leaves are triangular and hairy; these are formed when the plants do not produce normal green leaves. Alternate patches of scale leaves and leaf-bases form the characteristic ribbing on the stem. Bases of sporophylls

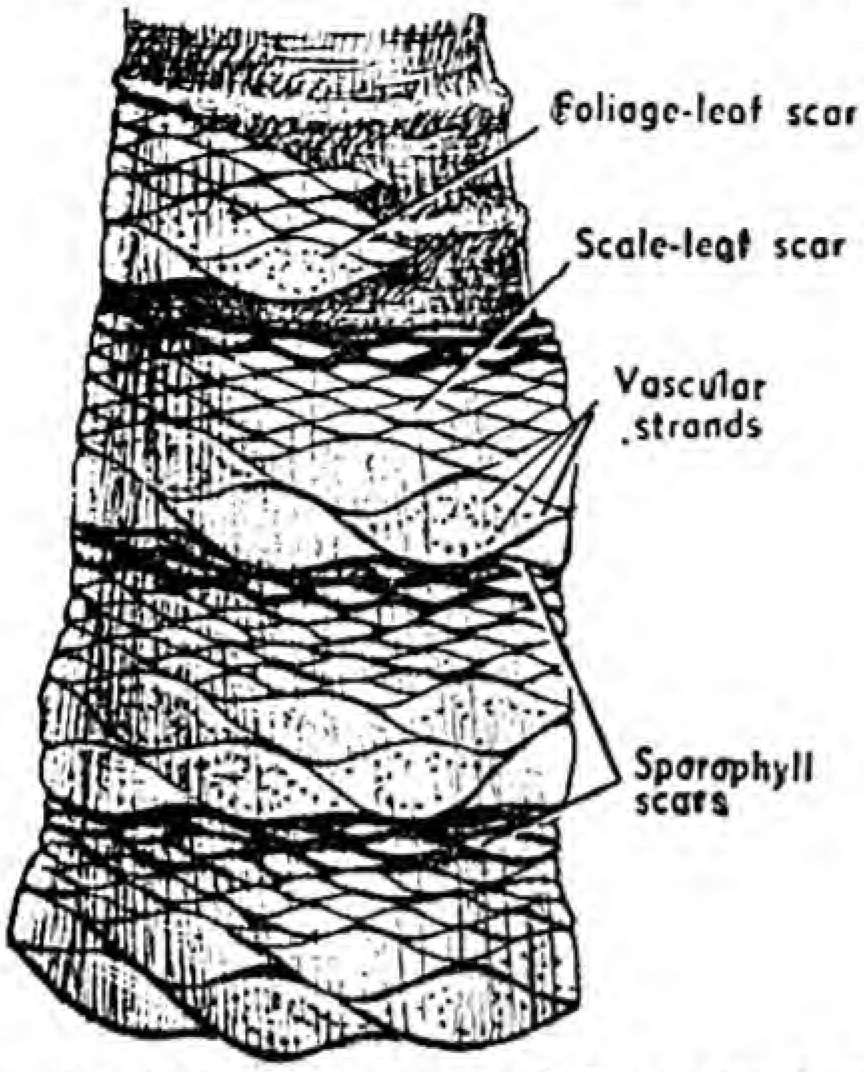


Fig. 4-12 An old trunk of *Cycas revoluta* showing different kinds of scars

1. Pant, D. D. & B. Mehra 1962.
2. Coulter, J. M. & C. J. Chamberlain 1910.
3. Pant, D. D. 1953.

are also present in older plants (fig. 4-12). Young leaves of *Cycas* show circinate vernation, a character which they share with ferns (fig. 4-13).

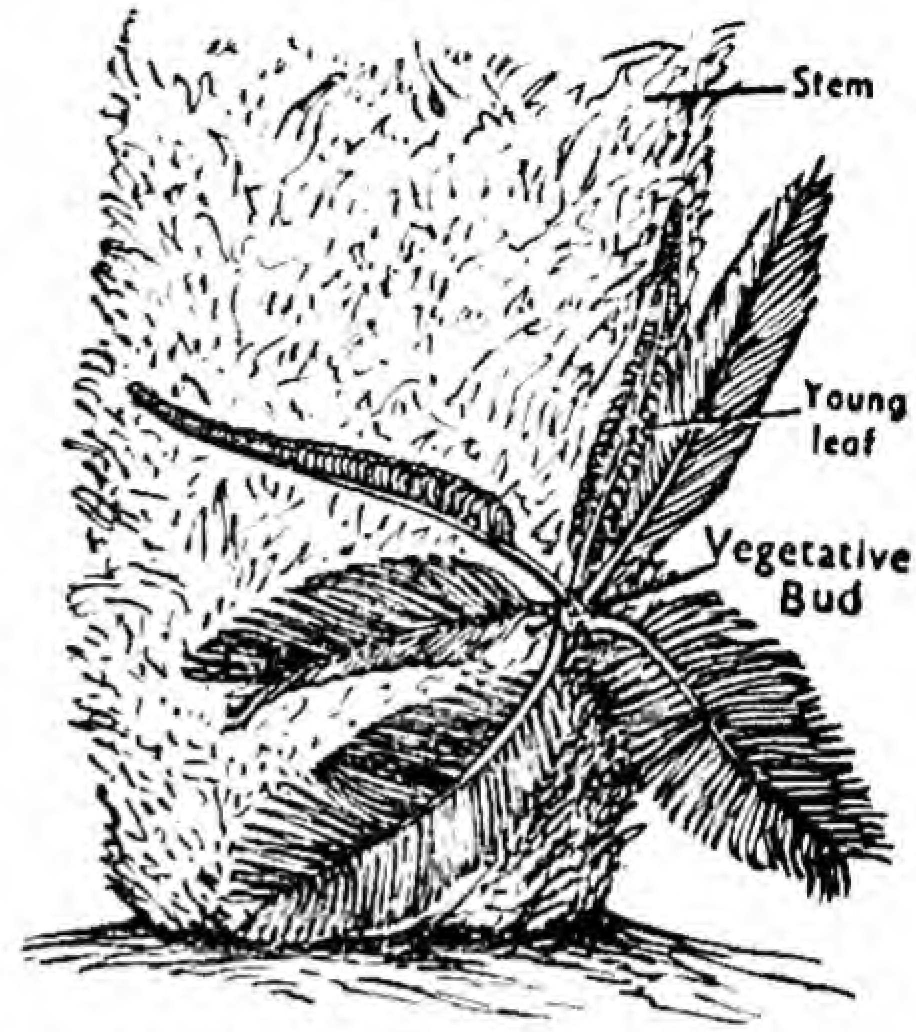



Fig. 4—13 Portion of a thick armoured trunk of *Cycas revoluta* with a young bud showing circinate vernation of leaves.

*Cycas* plants bear a tap root which is short lived and is later replaced by adventitious roots. In addition to these there also arise a few negatively geotropic lateral roots which are profusely and dichotomously branched. They are small, apogeotropic (fig. 4-14) and come out of the soil surface. They have bacteria, blue green algae and fungi in their cortex. The entry of these organisms is said to be responsible for the characteristic swollen, knob-like or coral-like appearance and hence the name, coralloid roots.

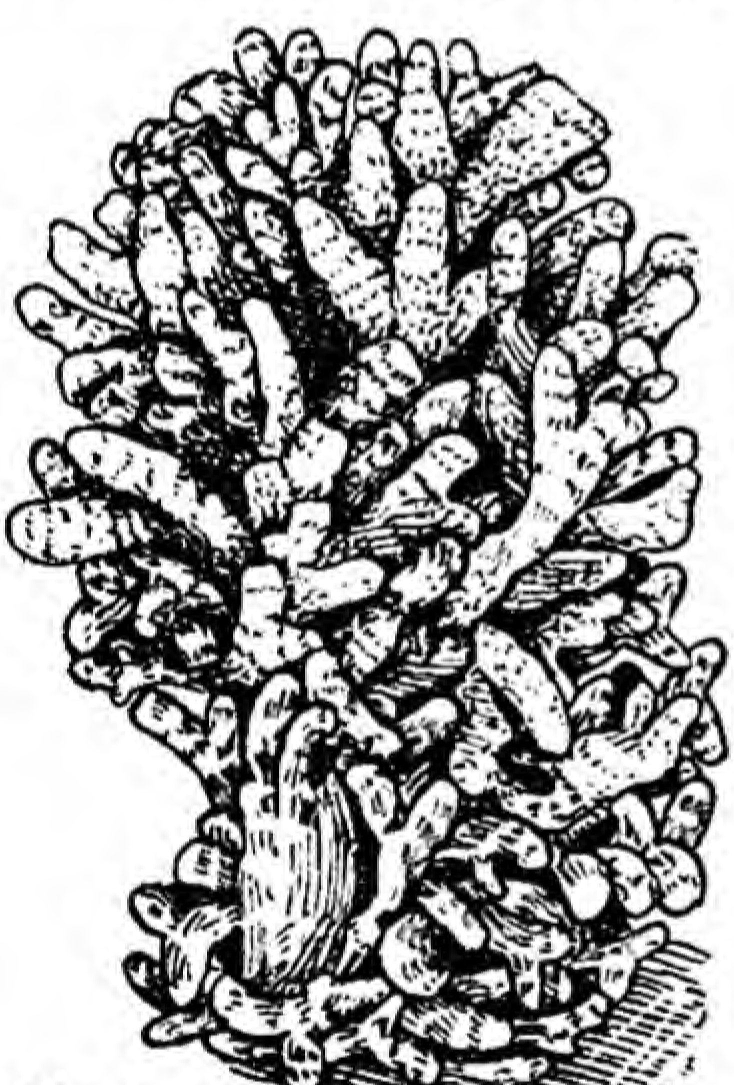


Fig. 4—14 Coralloid roots of *Cycas revoluta*.

VEGETATIVE PROPAGATION—In Japan, vegetative propagation of palms, cycads, etc., is practised as an art called 'bonsai', in which plants are injured at places to induce branching. The dwarfing habit is induced by successive artificial injuries. Adventitious buds or bulbils quite commonly arise on the trunk. These are used for vegetative propagation.

HISTOLOGICAL FEATURES—The root of *Cycas*, in young stage, possesses an outer thin layer, the epiblema followed by multilayered parenchymatous cortex containing mucilage canals which are lined by a layer of epithelial or secretory cells. Stele is

surrounded by a single layered endodermis possessing casparian strips and many layered pericycle. Vascular bundles are radial with two to four xylem patches which alternate with phloem. The protoxylem has spiral and the metaxylem scalariform thickenings and the latter sometimes possesses pitted elements. The

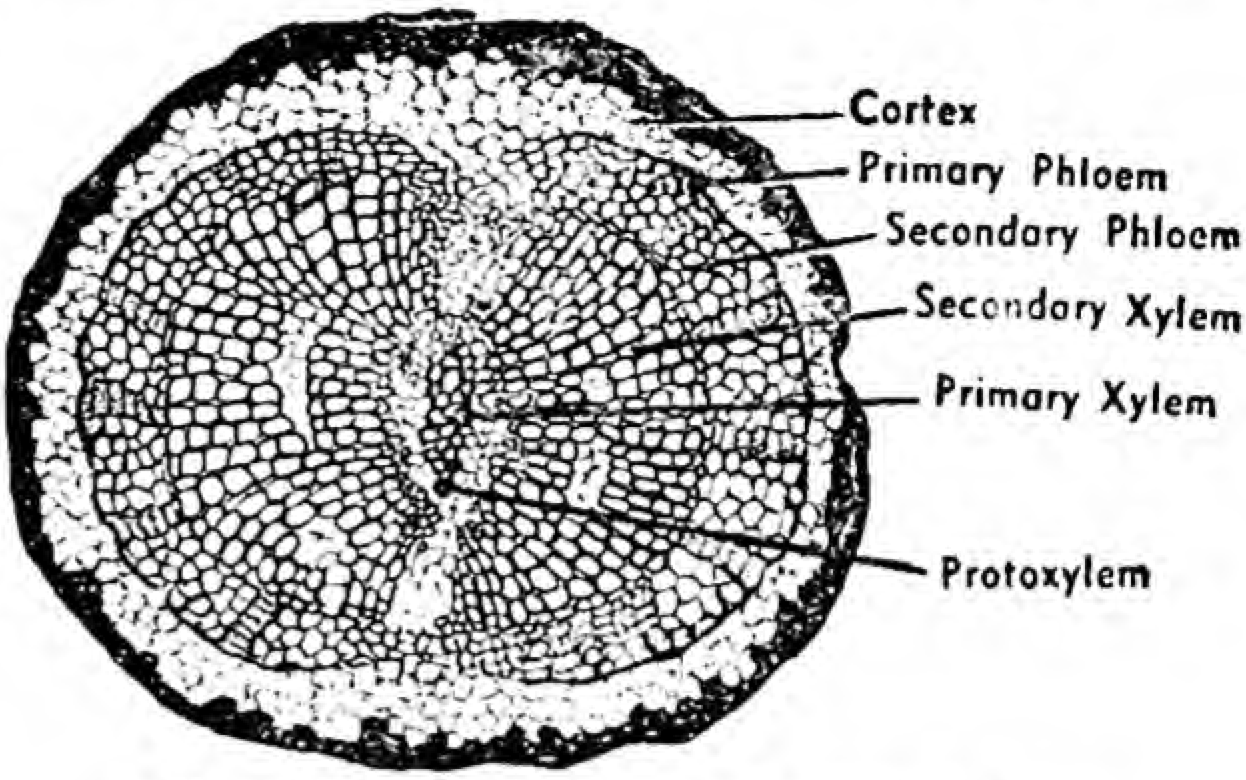



Fig. 4-15 T. S. of a diarch root of *Cycas revoluta* with secondary growth

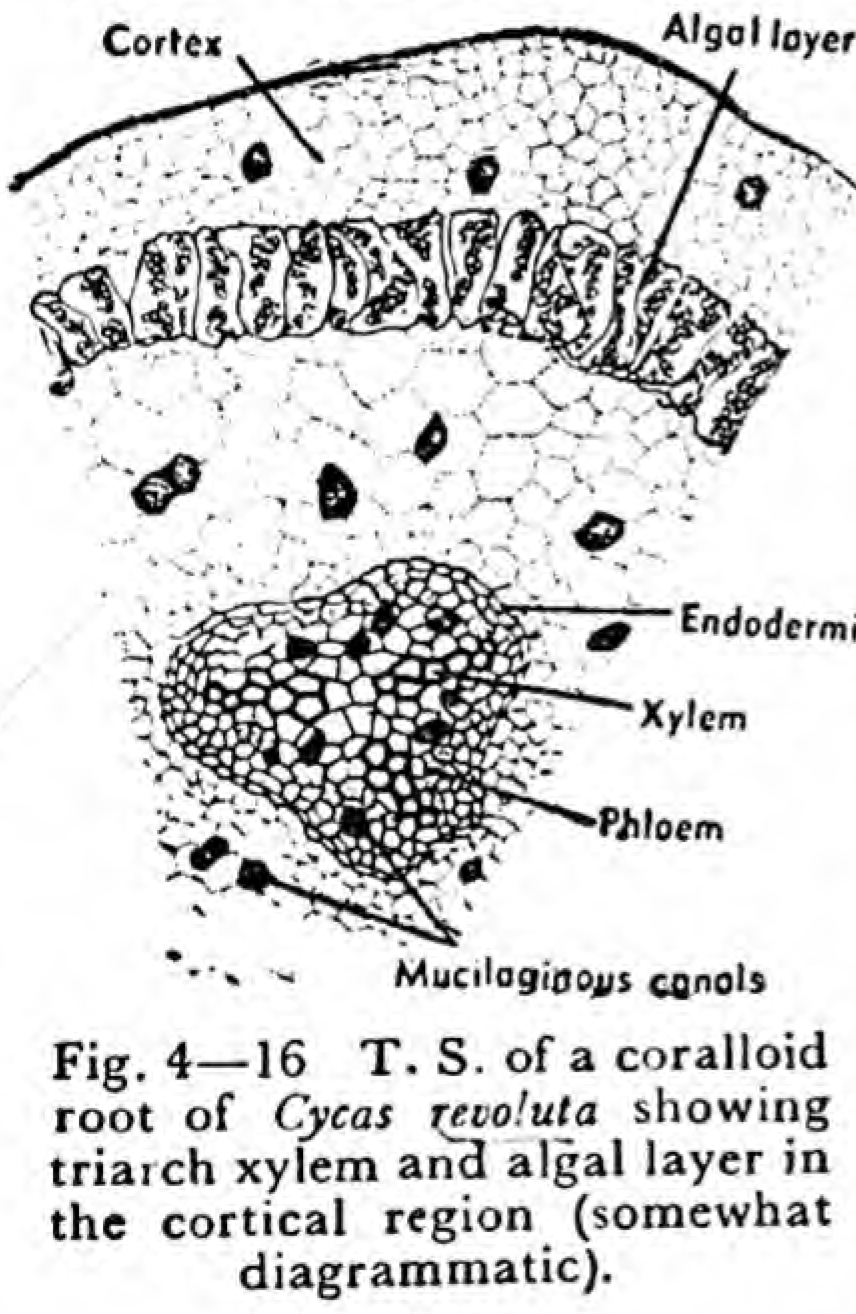



Fig. 4—16 T. S. of a coralloid root of *Cycas revoluta* showing triarch xylem and algal layer in the cortical region (somewhat diagrammatic).

protoxylem of stem, according to Greguss[1], has no spiral thickenings. Xylem is exarch (fig 4-15), but Atwood[2] reported the presence of mesarch protoxylem in the adventitious roots of *Cycas revoluta*; this, however, needs confirmation. Phloem in the young stage consists of parenchymatous tissue, but in older parts it consists of bast fibres. Coralloid roots usually have one or rarely more than one-layered thick algal zone (fig 4 16). The algal zone is absent from the roots penetrating into deeper layers of the soil. Coralloid roots possess poorly developed secondary tissues. Cells of algal zone usually possess *Anabaena cycadeae* and *Nostoc punctiforme*. Sometimes *Oscillatoria*, Diatoms, *Azotobacter* and *Pseudomonas* have also been found in these zones (fig. 4-16). Chaudhuri and Akhtar[3] have reported dichotomous mode of branching in some of these roots.

1. Greguss, P. 1955.
2. Atwood, S. 1935.
3. Chaudhuri, H. & A. R. Akhtar 1931.

The stem assumes an irregular outline in cross section because of the presence of numerous leaf-bases. The epidermis is not clearly demarcated. The stem consists of a wide parenchymatous, multilayered cortex which is full of starch besides having numerous mucilage ducts and leaf traces (fig. 4-17). The vascular cylinder is eustelic like of that of a dicotyledonous angiosperm. Vascular bundles are collateral, open and endarch. Pith is centrally situated (fig. 4-17). It is parenchymatous and full of starch. In *Cycas* seedling, xylem is mesarch. Xylem rays occur in between the two adjacent xylem bundles, they are broad and deep. Leaf-traces are small, endarch inside the stem but as they enter the leaf, they become pseudomesarch due to the formation of the centripetal xylem; at the extreme tip of the rachis they are said to become exarch.

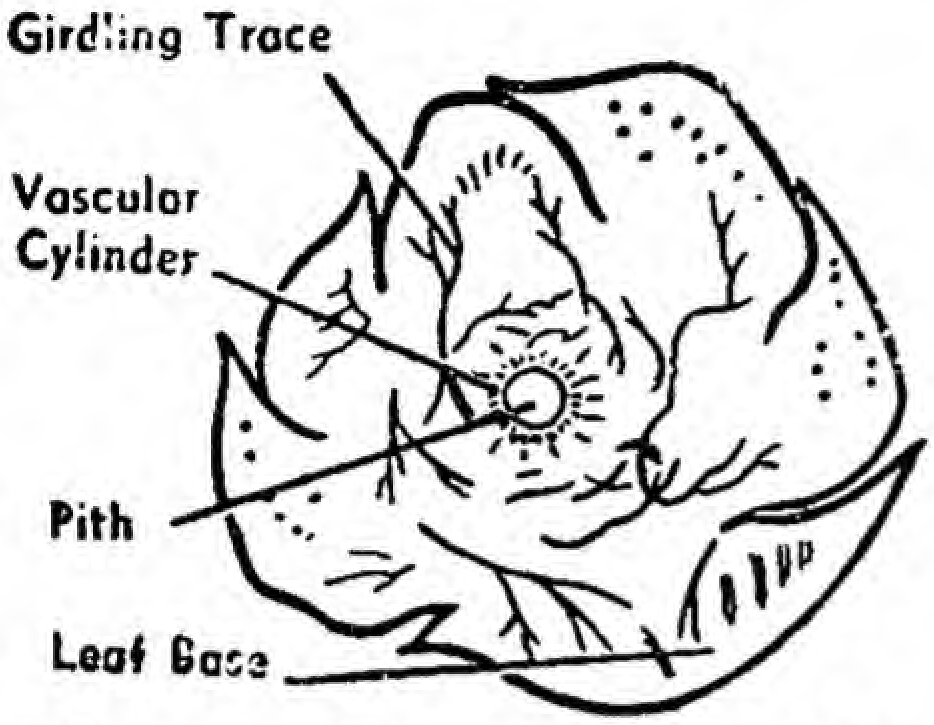



Fig. 4—17 Outline sketch of the T.S. of a young stem of *Cycas* showing girdling traces (After Engler and Prantl).

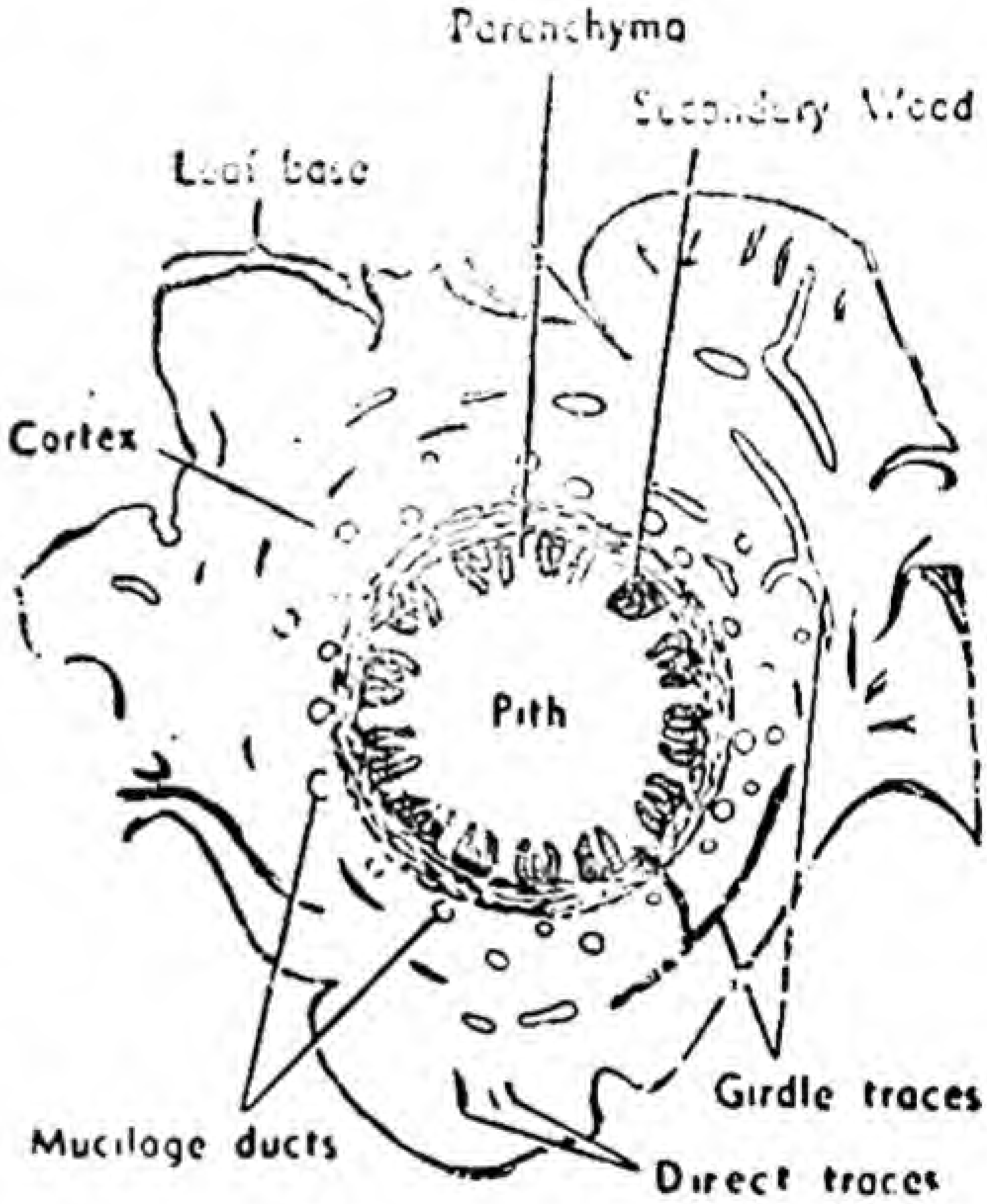



Fig. 4—18 T. S. of a young stem of *Cycas revoluta* with vascular bundles arranged in a ring, girdling traces and mucilage ducts.

The leaf-traces in the stem of *Cycas* (fig. 4-18) arise from the vascular bundles of the primary ring. Each leaf is supplied with two main leaf-trace bundles and several small radial bundles. The two trace bundles may either arise independently or may be formed by the branching of one and the same trace. Traces arise from the protoxylem of the primary vascular ring, opposite the leaf which

they supply. The leaf trace first passes obliquely outwards through the cortex, then it divides into two halves, each half running round in opposite direction in the cortex later meeting at the base of the leaf and after bending out going into the petiole. Because these traces go round the stem, they are called 'girdling traces' or 'indirect traces' (fig. 4-18). Direct traces or bundles also arise from the primary ring; these in turn bifurcate and each half produces a complex system of anastomosing bundles. They get attached to the girdle bundles, both of their own and of other leaves, in the same group. Hence the leaf-trace of each group of leaves forms a single united system. The girdle as well as direct-traces anastomose together, they then enter the leaf-bases, where they branch freely and arrange themselves in the form of a 'U' characteristic of the petiole (fig. 4-23).

Presence of girdle bundles is a characteristic feature of the Cycadales. McLean and Cook[1] suggest a possible relationship between the Cycadales and *Liriodendron* Linn. (Magnoliaceae) on the basis of such traces, but the origin of traces in the two groups has been found to be altogether different from and independent of each other.

A leaf-trace, when it enters the petiole is normally collateral, the xylem consisting of rows of tracheids, separated by rays. The metaxylem is entirely centrifugal. Protoxylem, therefore, at this stage is endarch. A little higher up in the petiole, the centrifugal xylem gets gradually reduced. The centripetal xylem makes its appearance on the other side of protoxylem opposite the centrifugal xylem. This changes the endarch nature of the petiolar bundle which for most of the length of the rachis maintains this character. The rachis as well as the pinnae of *Cycas* possess vascular bundles in which the centrifugal metaxylem develops secondarily and it is also separated from protoxylem by a small amount of parenchyma. Such bundles are spoken of as mesarch, although in the strict sense, they are pseudomesarch or diploxylic (fig. 4-23 & 4-24). At the extreme tip of rachis the centrifugal xylem is said to be completely reduced hence the protoxylem can be said to be exarch in position. This, however, needs confirmation.

**Secondary growth**—In the roots of *Cycas* abnormal type of secondary growth takes place by the formation of cambial arcs

1. McLean, R. C. & W. R. Ivimey Cook 1951.

along the inner edges of phloem strands, which soon cut off secondary xylem on their inner and secondary phloem on their outer faces. Xylem rays are formed and primary phloem gets ultimately crushed. The two cambial arcs go on adding secondary tissues, they also meet each other and thus a continuous cylinder of secondary vascular tissue is formed (fig. 4-19). While this is happening, a distinct layer of phellogen arises in the cortex, which cuts off the phelloderm on the inner and phellem on the outer side of the phellogen. In certain anomalous cases more than one layer of cambia may be formed.


Fig. 4—19 Portion of the T. S. of an old stem of *Cycas* with two rings of secondary wood (After Pant and Mehra)

The young stem of *Cycas* shows normal secondary growth like that of dicotyledonous angiosperm by the activity of intra-and interfascicular cambia. These cut off secondary xylem on the inner and secondary phloem on the outer sides (fig. 4-18). Secondary rays and parenchyma cells are radially distributed in secondary xylem (fig. 4-20). Secondary phloem possesses fibres and sieve cells. deBary[1] and Miller[2] report the presence of sieve tubes in the phloem and Greguss[3] that of

1. deBary, A. 1884 2. Miller, W. L. 1919. 3. Greguss, P. 1958.

the vessels in the secondary xylem of *C. revoluta*, but this needs confirmation. In *Cycas*, metaxylem tracheids have elongate broad borders with apertures which are obliquely to transversely oriented in relation to cell wall. Bierhorst[1] states that in secondary xylem the bordered pits are round. Sifton[2] reported the presence of the rims of Sanio in *C. revoluta*. The pits may be in two or three series, alternate, sometimes they may be pressed and appear angular like those in the Araucariaceae. There may be 8 to 12 bordered pits in the field (fig. 4-21). Greguss[3] noted a kind of spiral structure in the secondary tracheids of *Cycas* which probably has nothing in common with the tertiary spiral of *Taxus* (fig. 4-21). Extrastelar secondary growth takes place by the formation of phellogen which cuts off phelloderm on its inner side and phellem towards the periphery. Lenticels are also formed.

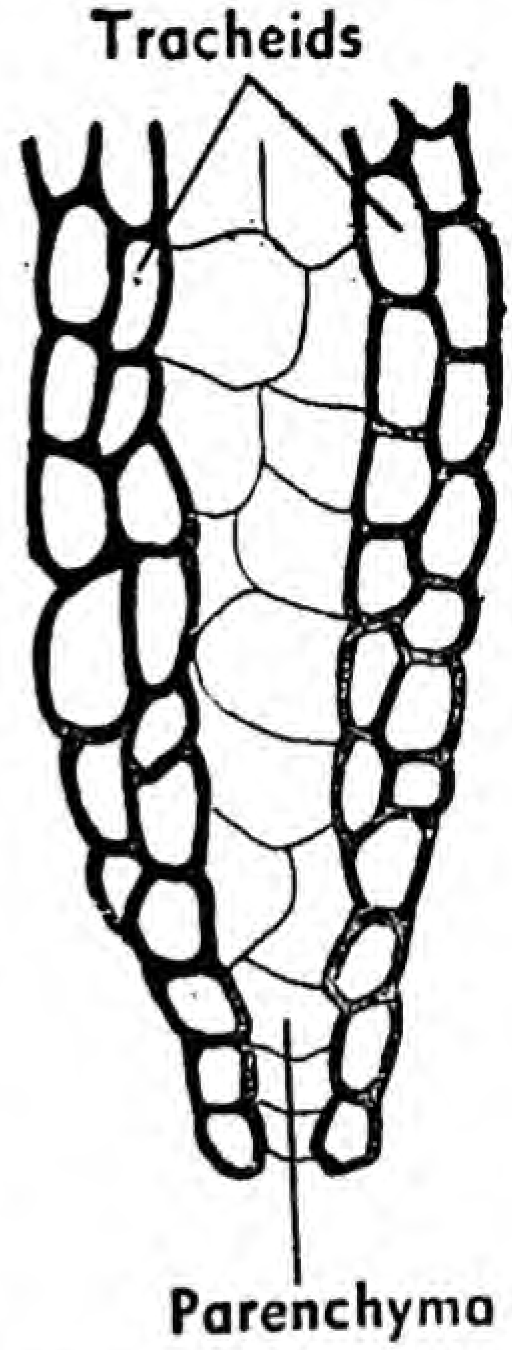


Fig. 4—20 Wood tracheids and ray parenchyma in T. S. of *Cycas* (highly enlarged).

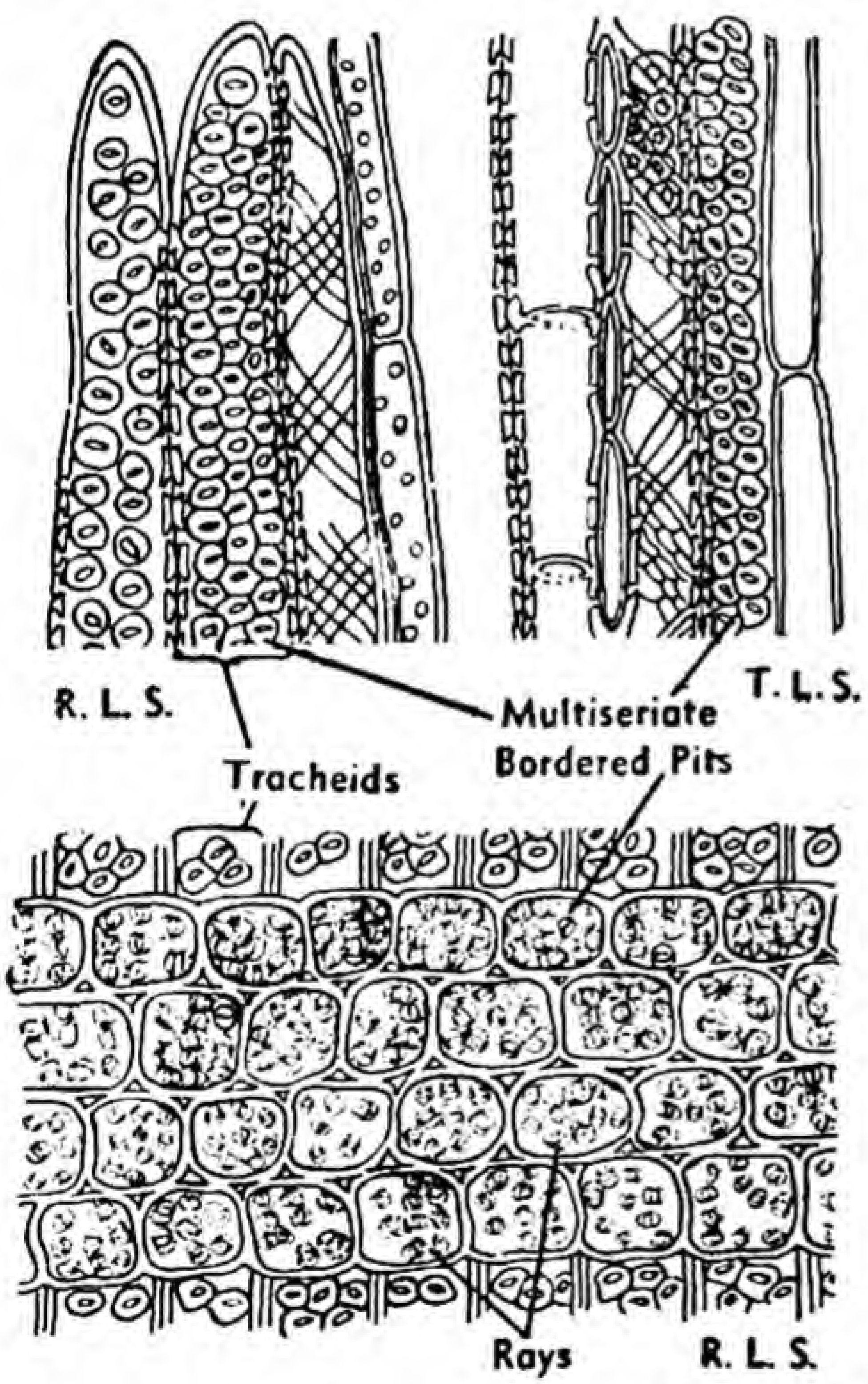


Fig. 4—21 Portions of secondary wood of *Cycas* in longitudinal sections showing multiseriate pitting (After Greguss).

The cortex, Xylem rays and pith in a young stem of *Cycas* are in larger proportion and more prominent as compared to the conducting zone, the xylem. The stem, therefore, is soft and spongy, hence it is sometimes called 'manoxylic', in contrast to the wood of conifers where the ratio of xylem

1. Bierhorst, D. W. 1960. 2. Sifton, H. B. 1915. 3. Greguss, P. 1955.

to such tissues is much larger making the conifer wood more compact, or 'pycnoxylic'.

In fairly old plants secondary growth is of abnormal or anomalous type. In the beginning, the stem is monoxylic (single ring of vascular bundles), but later several concentric rings of vascular bundles develop and the stem then becomes polyxylic (fig. 4-22). The zones of xylem and phloem are formed at irregular intervals. The cambium of the first ring remains active for only a short time and is succeeded by another zone of cambium which is formed independently in the pericycle or the cortex. This may be superseded by a third, fourth or fifth cambial layer. Chamberlain[1] counted fourteen rings in the stem of *C. pectinata*. Sometimes, it

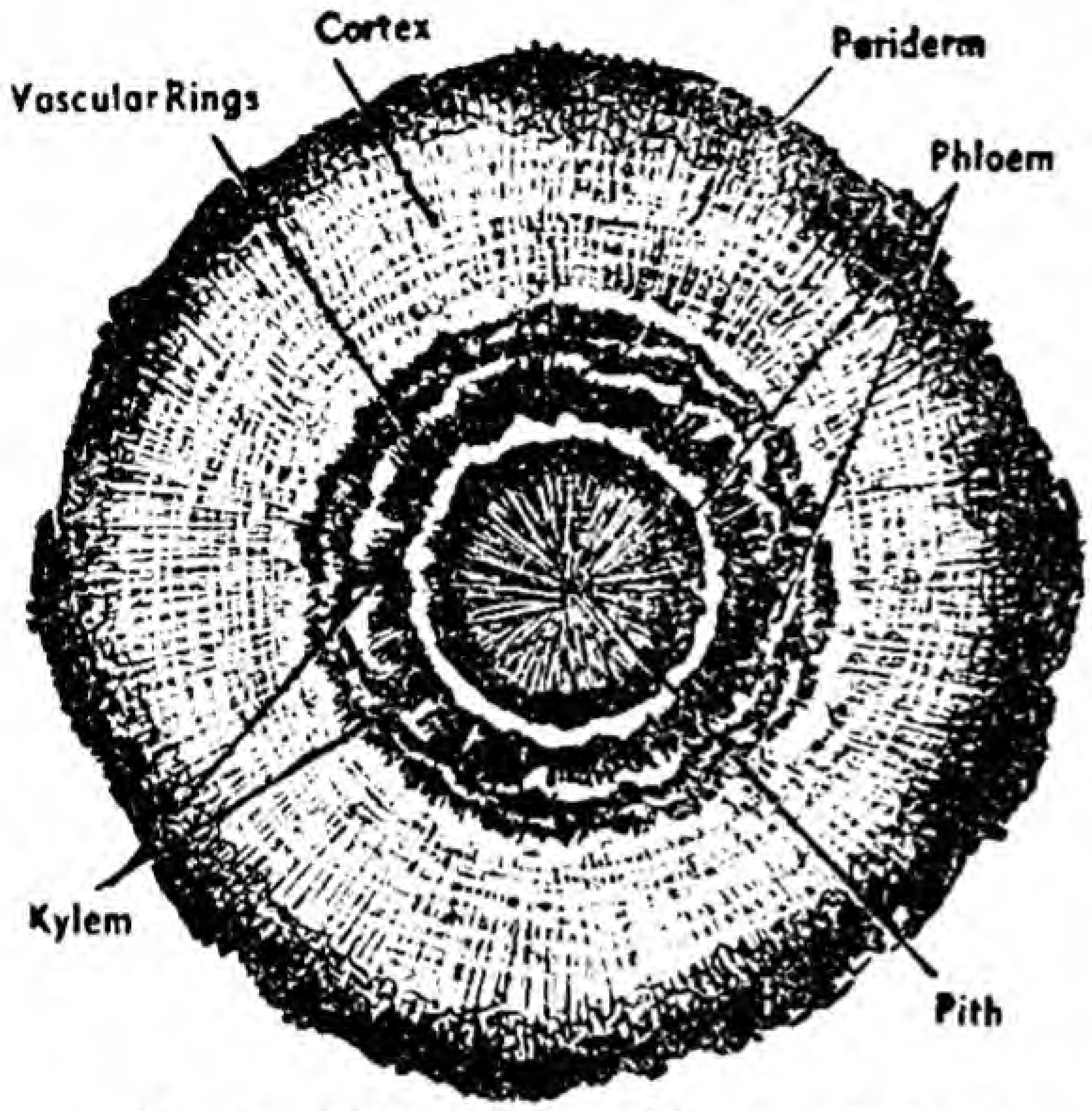


Fig. 4—22 T. S. of an old stem of *Cycas* showing polyxylic condition.

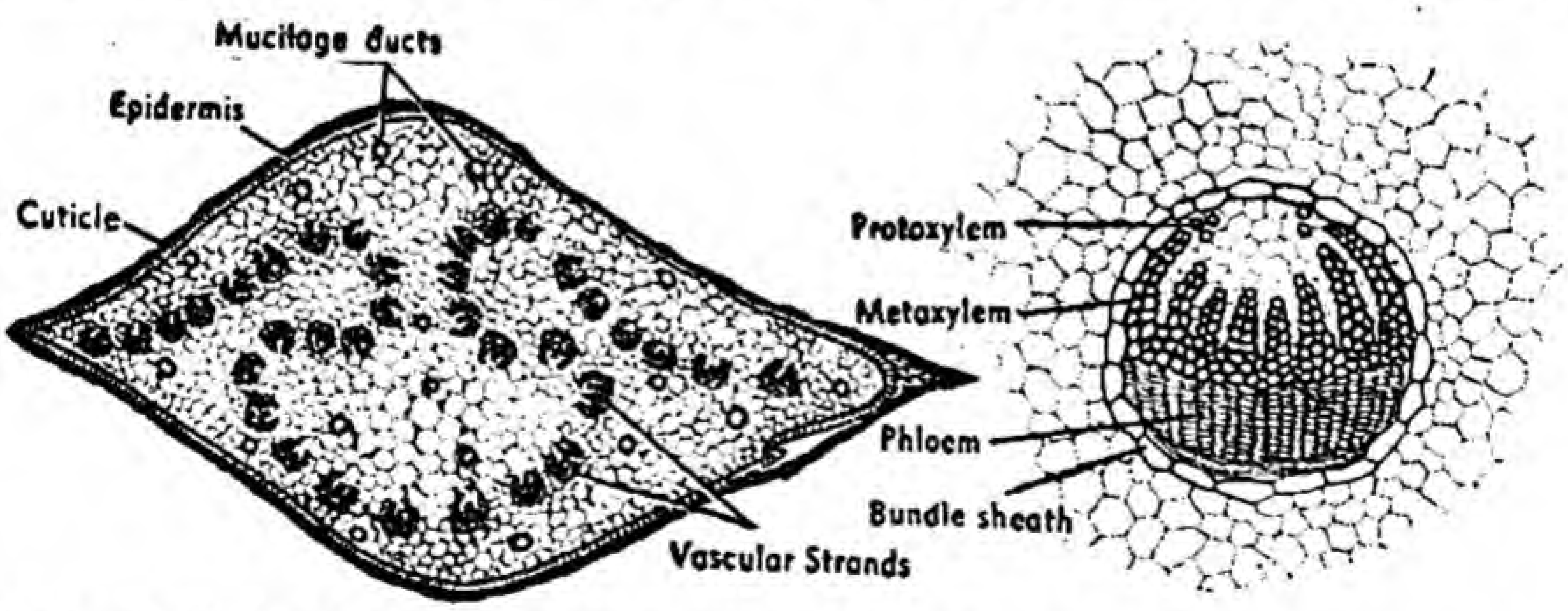


Fig 4—23 T. S. of the rachis of *Cycas revoluta* at the base showing mucilage ducts and endarch protoxylem. Centripetal metaxylem has not yet developed. A single vascular bundle has been enlarged to show the internal details.

has been observed that in *Macrozamia* and *Bowenia* the cambia that arise in between two rings (tertiary cambia) produce tissues

1. Chamberlain, C. J. 1935.

with reverse orientation, i. e., phloem inwards (towards the centre) and xylem outwards (away from the centre) of the stem.

The petiole may be cylindrical or flattened in cross section with several mucilage canals arranged in a ring. The vascular bundles are arranged like the letter 'U' (fig. 4-23). The flanges of the arms pass into leaflets. The ground tissue is made up of outer hypodermal zone of sclerenchymatous and inner zone of parenchymatous cells. Each vascular bundle (fig. 4-23 & 4-24) is enclosed by a bundle sheath inside which is present the

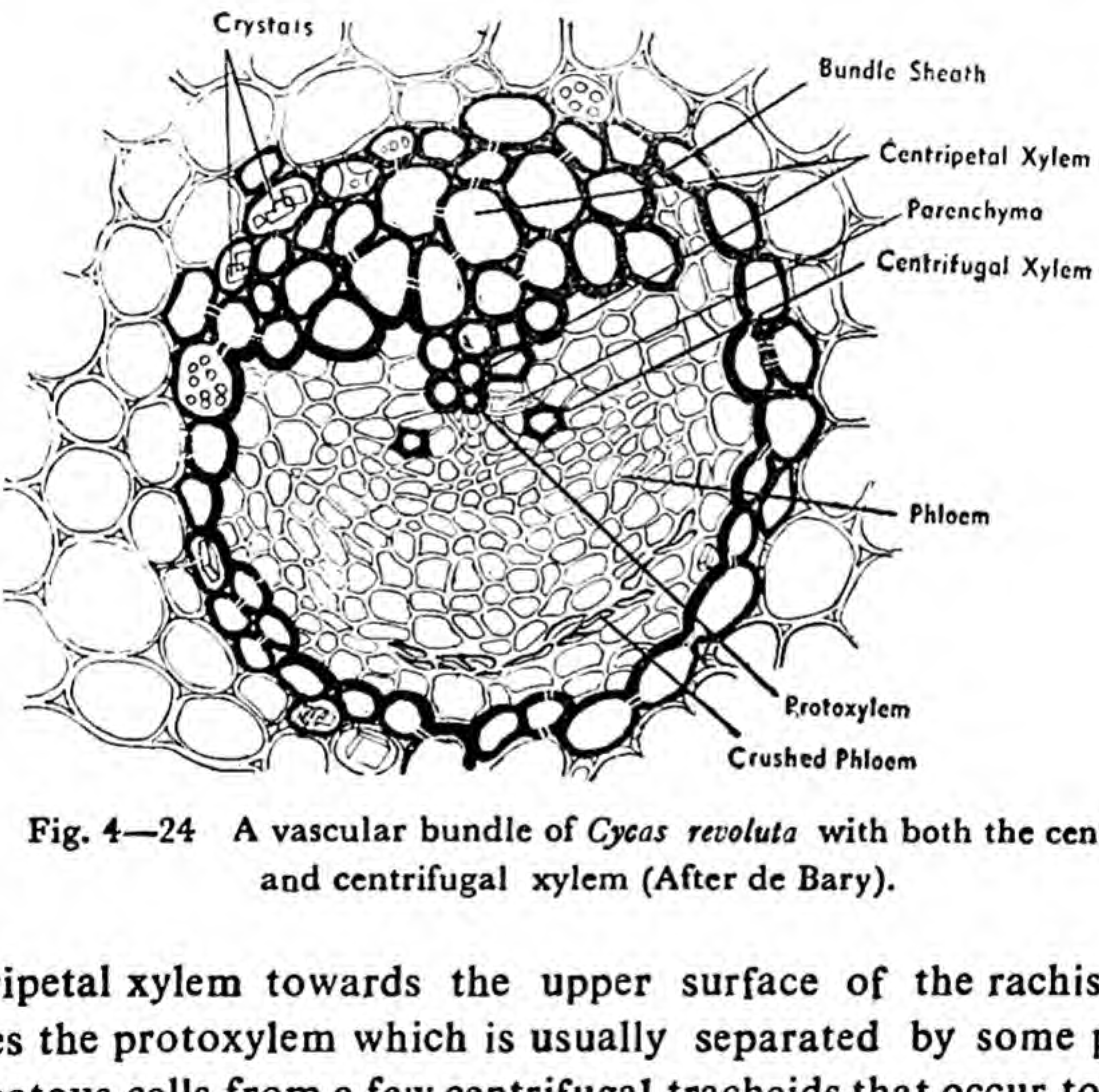



Fig. 4—24 A vascular bundle of *Cycas revoluta* with both the centripetal and centrifugal xylem (After de Bary).

centripetal xylem towards the upper surface of the rachis, then comes the protoxylem which is usually separated by some parenchymatous cells from a few centrifugal tracheids that occur towards the phloem. Probably a little cambium is present between the phloem and the centrifugal xylem. It is stated that these centrifugal elements are secondarily formed hence the bundle is in strict sense 'diploxylic' or 'pseudomesarch'. The rachis has an outermost covering of thick walled epidermis which is provided with a thick cuticle. Stomata are irregularly distributed on the epidermis.

The vascular bundles of the rachis frequently dichotomise and anastomose in their longitudinal course. Bundles which lie at the

3668
2768

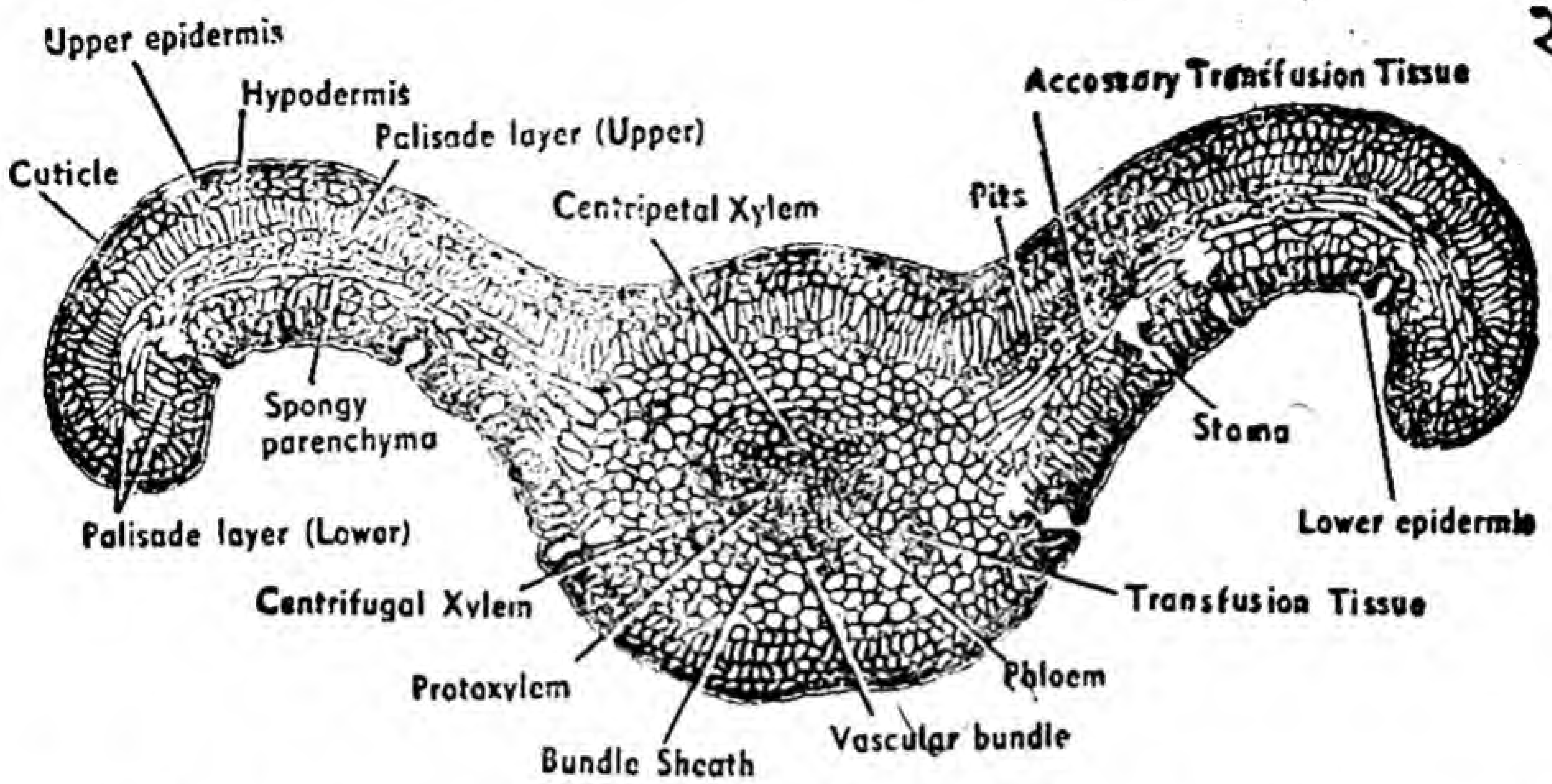



Fig. 4—25A. T. S. of a pinna of *Cycas revoluta* with curved margins showing details of the internal structure.

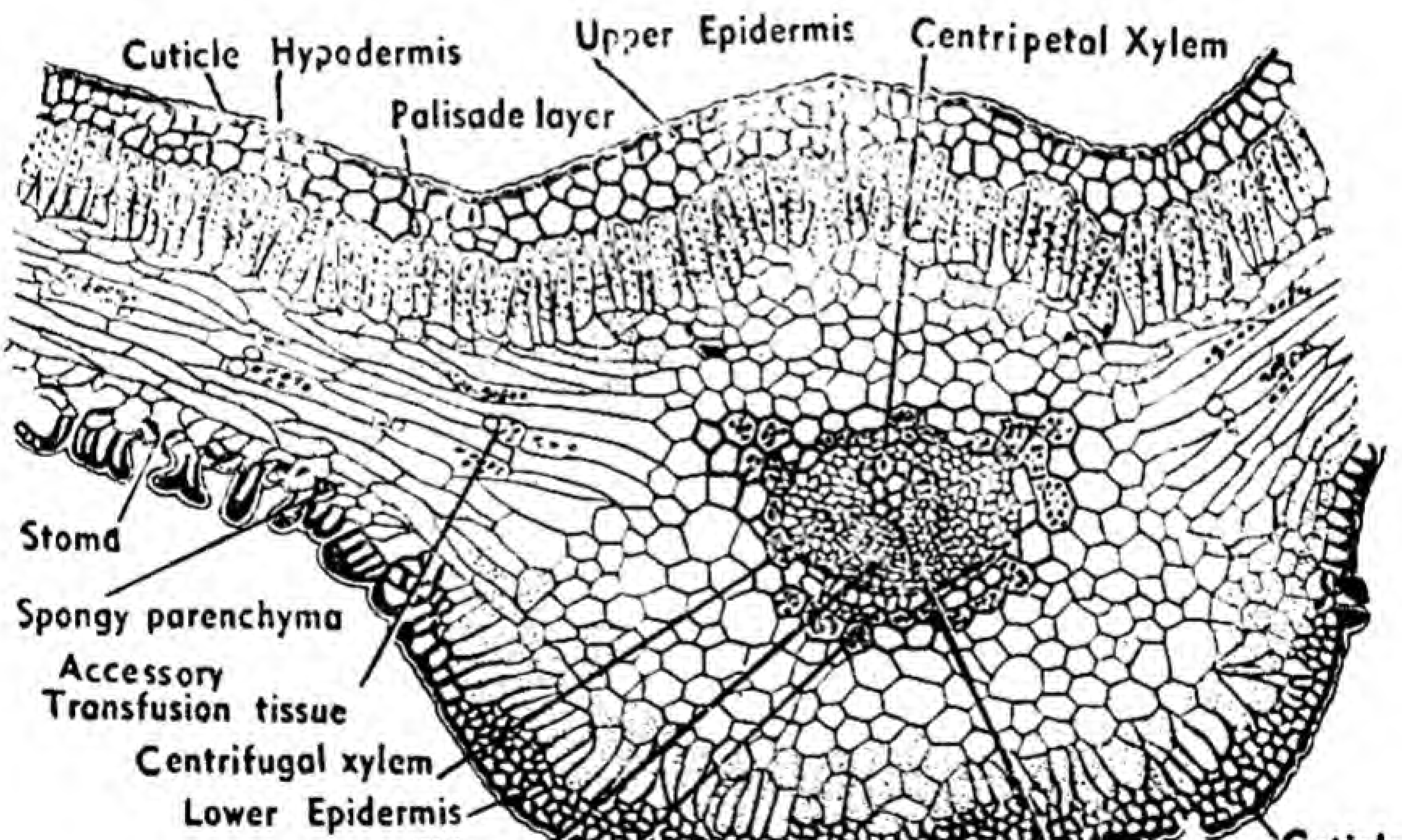



**Fig. 4—25B. Midrib and a portion of lamina (enlarged) of the T. S. of the pinna of *Cycas revoluta*.**

two open ends of the 'U' pass out and enter the two pinnae. This is continually repeated till, near the apex of the rachis, only a few

vascular bundles remain ; these are arranged in a 'C'-shaped arc. Ultimately one by one, these bundles too enter the terminal pinnae of the leaf.

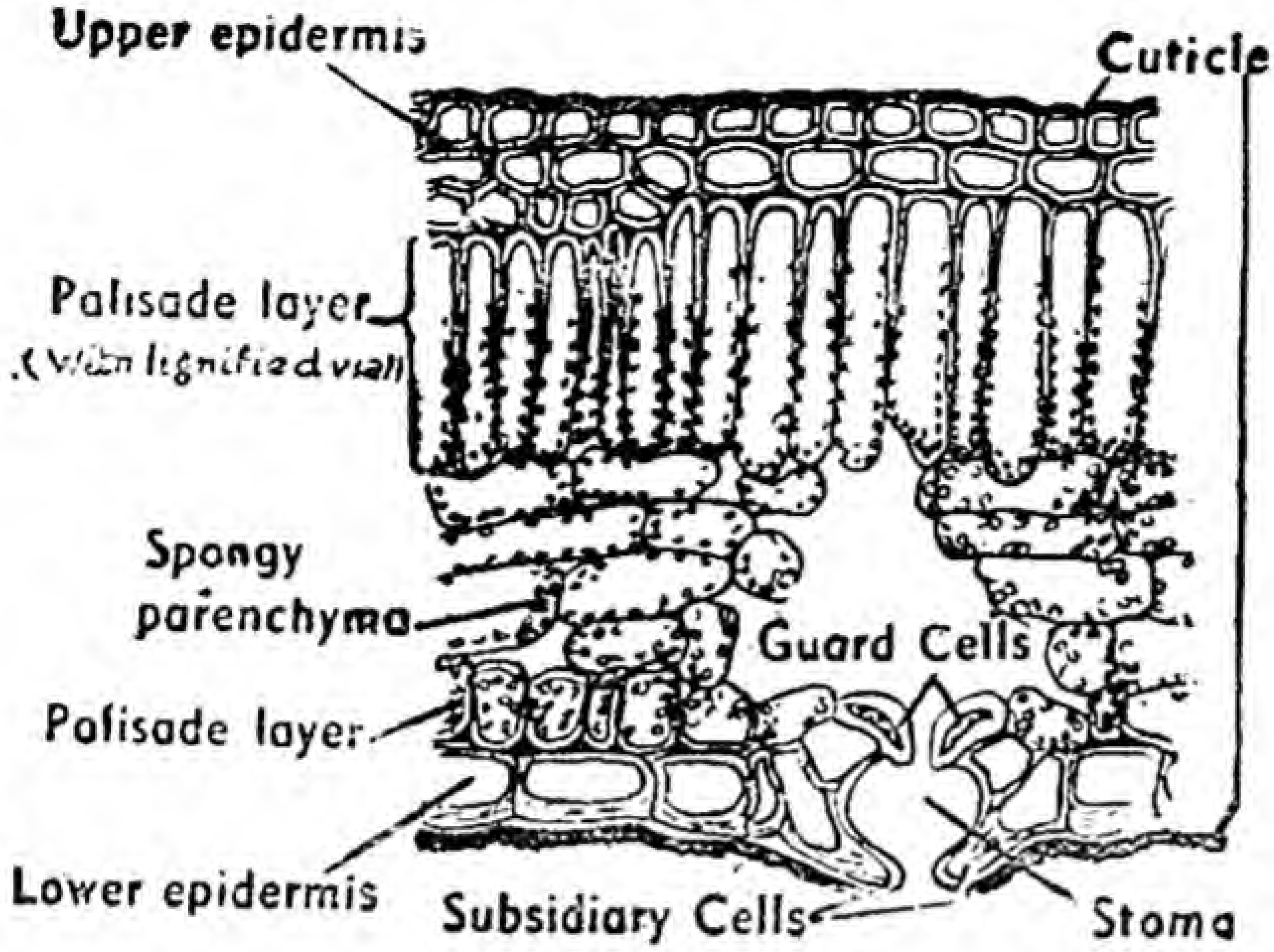



Fig. 4—26 T. S. a portion of the pinna of *Cycas* (enlarged) showing lignified palisade layer and the spongy tissue. Stomata are present on the lower surface only (After Esau).

The leaflets or pinnae of *Cycas* are dorsiventral and hypostomatic (stomata present on lower surface only). In transection of the pinna a thick cuticle is followed by a thick-walled epidermis. Stomata occur on lower side of the leaf and are sunken (fig. 4-25 & 4-26). Below the epidermis occurs the sclerenchymatous hypodermis. Palisade tissue consists of elongated cells full of chloroplasts. The palisade tissue of *Cycas* leaf, according to Eames and McDaniels[1], has lignified walls, the thickenings gradually diminishing towards the lower end which may have no lignin (fig. 4-26). The middle part of the pinna is filled with spongy parenchyma.

Separated by some parenchyma cells, or directly in contact with the centripetal xylem, abutting on the bundle sheath, is the transfusion tissue (fig. 4-25A&B). The cells of this tissue are short and wide with walls that have reticulate or bordered pitted thickenings. Worsdell[2] thought that transfusion tissue was the lateral extension of centripetal xylem but Carter[3] derives it from leaf parenchyma. Takeda[4] regarded it as a mere physiological modification of pericycle or mesophyll cells for the storage of food. In between the

1. Eames A. J. & L. H. McDaniels 1947.
2. Worsdell, W. C. 1897.
3. Carter, M. G. 1911.
4. Takeda, H. 1913.

mesophyll cells also occur a few tracheid-like, colourless, lignified cells, having bordered pits on their walls. These are arranged at right angles to the axis of the leaf and constitute the so-called radial parenchyma, secondary transfusion tissue, hydrostereom or accessory transfusion tissue (fig. 4-25 A & B). It is connected with the xylem through the transfusion tissue and represents, according to Lignier[1], the reduced lateral conducting strand.

Vascular bundles are surrounded by a jacket of thick-walled cells. Phloem lies towards the lower leaf-surface. Protoxylem is pseudomesarch or diploxylic. The centripetal xylem is directed towards the upper leaf-surface and the centrifugal xylem towards the lower. Opening and closure of stoma is regulated by two subsidiary cells (fig. 4-26). In *C. revoluta* the sunken stoma is amphicyclic, i. e., it is surrounded by a ring of subsidiary cells and opens into a cavity.

## LIFE-HISTORY

The plants of *Cycas* are dioecious, i. e., male and female reproductive organs occur on different individuals. Male

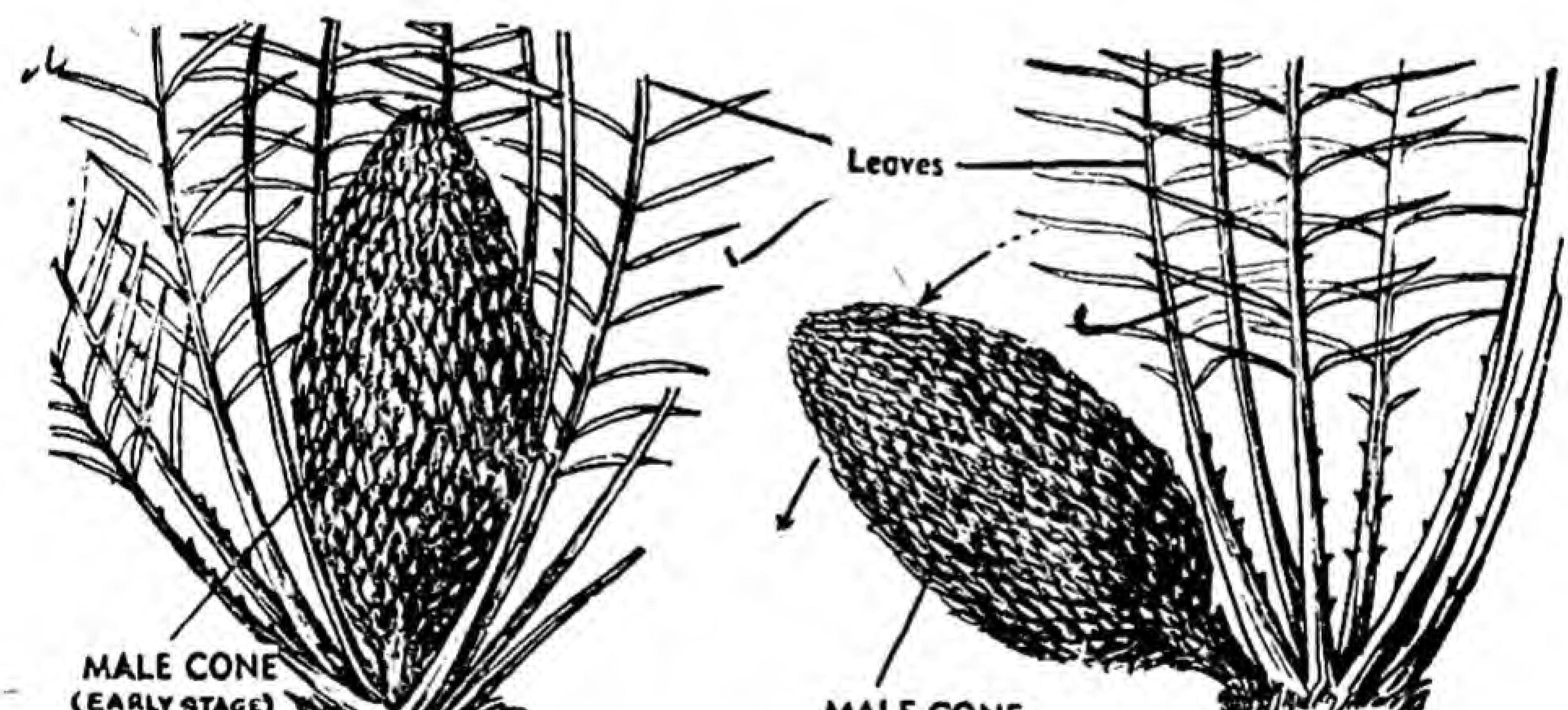



Fig. 4—27 A male strobilus (cone) of *Cycas* at young (early) and mature (late) stages of development.

strobilus develops terminally and thus uses the stem apex. Accordingly the stem in male plant of *Cycas* is 'sympodial' (fig. 4-27). In the female plant the megasporophylls are spirally

1. Lignier, O. 1892.

arranged like the foliage leaves, the growth of the stem, therefore, is continuous or 'monopodial'.

**Megasporophylls**—In *Cycas* there does not occur a true female strobilus. The megasporophylls are loosely arranged in acropetal

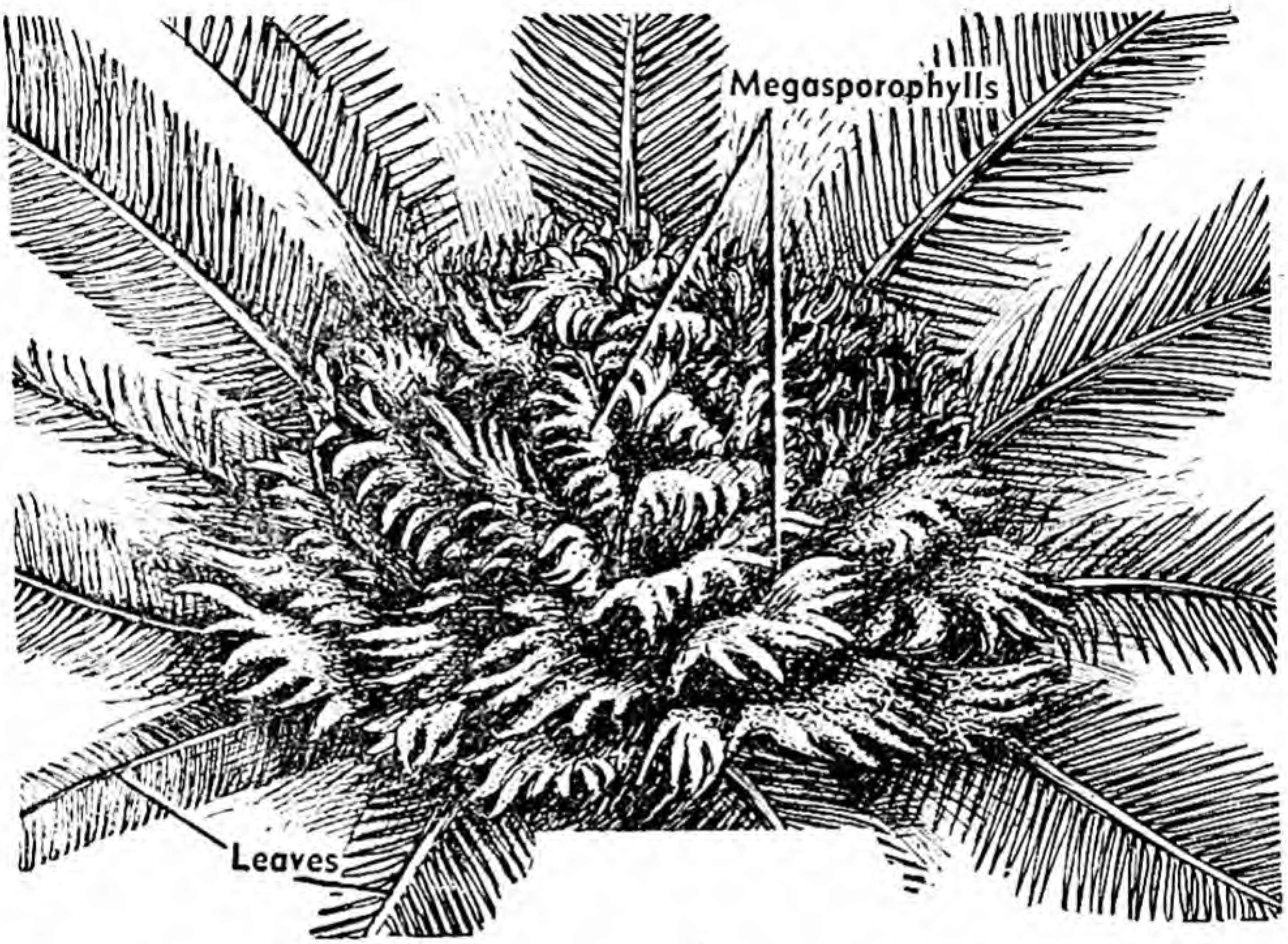



Fig. 4—28 Megasporophylls of *Cycas revoluta* (After Wettstein).

succession, leaving the apical meristem unaffected. They appear like a rosette (fig. 4-28). Megasporophylls develop when the plants are somewhat mature and are formed once a year. Their number in each whorl is more numerous in comparison with the foliage leaves. Each megasporophyll in *C. revoluta* measures 15 to 20 cm. in length; it is pinnate above (fig. 4-29 & 4-30) and the lower portion bears 2 to 12 ovules (1-6 on either side). The pinnate portion, resembling leaflets, is comparatively reduced in *C. circinnalis* (fig. 4-30).

**Development of Ovule**—De Silva and Tambiah[1] state that in *C. rumphii* 4 to 6 marginal protuberances appear on the megasporophyll superficially, while the megasporophyll itself is still covered

1. De Silva, B. L. T. & M. S. Tambiah 1952.

over by the scale leaves. The cells of these superficial protuberances divide to form the nucellus. The surrounding envelope (=integument) arises as a ring-like outgrowth round the nucellus at the base. Afterwards, the lower part of envelope fuses with the nucellus while the upper grows round the nucellus and almost completely covers it except for leaving a narrow passage at the apex called the micropyle. The apex of the nucellus does

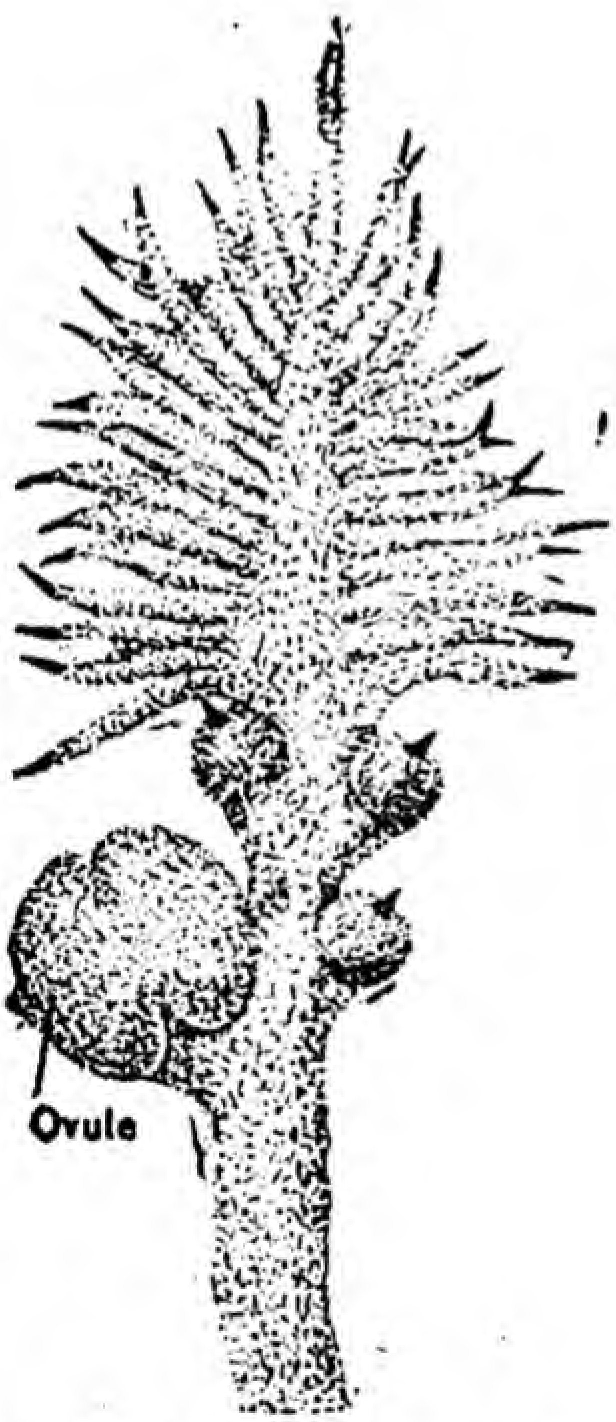



Fig. 4—29 A megasporophyll with ovule of *Cycas revoluta* (After Wettstein).

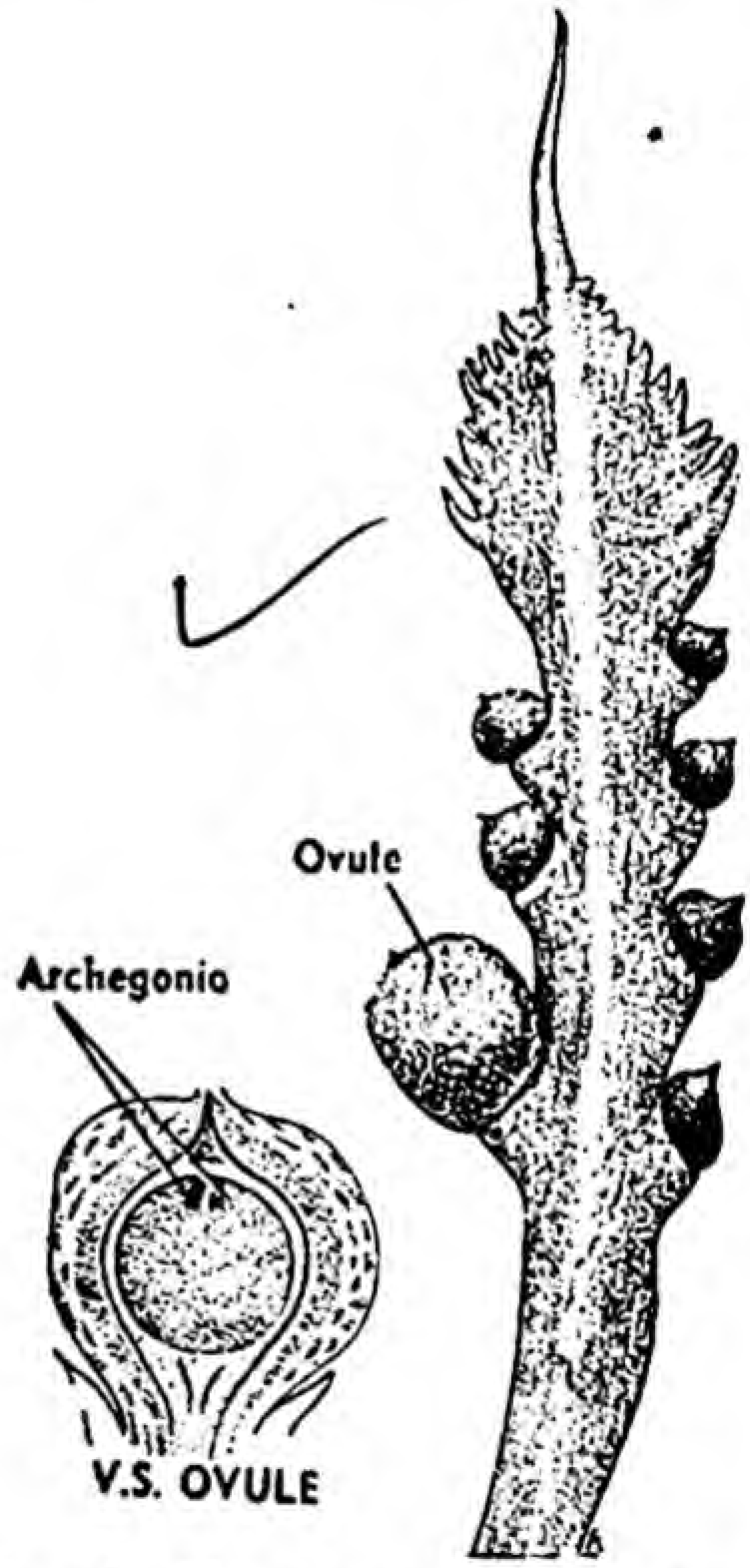



Fig. 4—30 A megasporophyll with ovules of *Cycas circinnalis*. The inset is the V. S. of ovule with two archegonia (After Wettstein).

not fuse with the envelope. It protects the megasporangium. The envelope, nearly 1 cm. thick in *C. circinnalis*, consists, of an outer and an inner fleshy and a middle stony layers. After fertilization the outer layer gets transformed into seed coat or testa (fig. 4-31). The outer fleshy layer is also called the sarcotesta; the middle stony one the sclerotesta and the inner fleshy layer the inner sarco-

testa. The sclerotesta possesses 2 to 3 ridges. The inner fleshy layer (inner sarcotesta), composed of parenchymatous cells except at the apex, is consumed in the development of the ovule and persists as a thin papery layer. The envelope remains in close contact with the nucellus except at the apical region

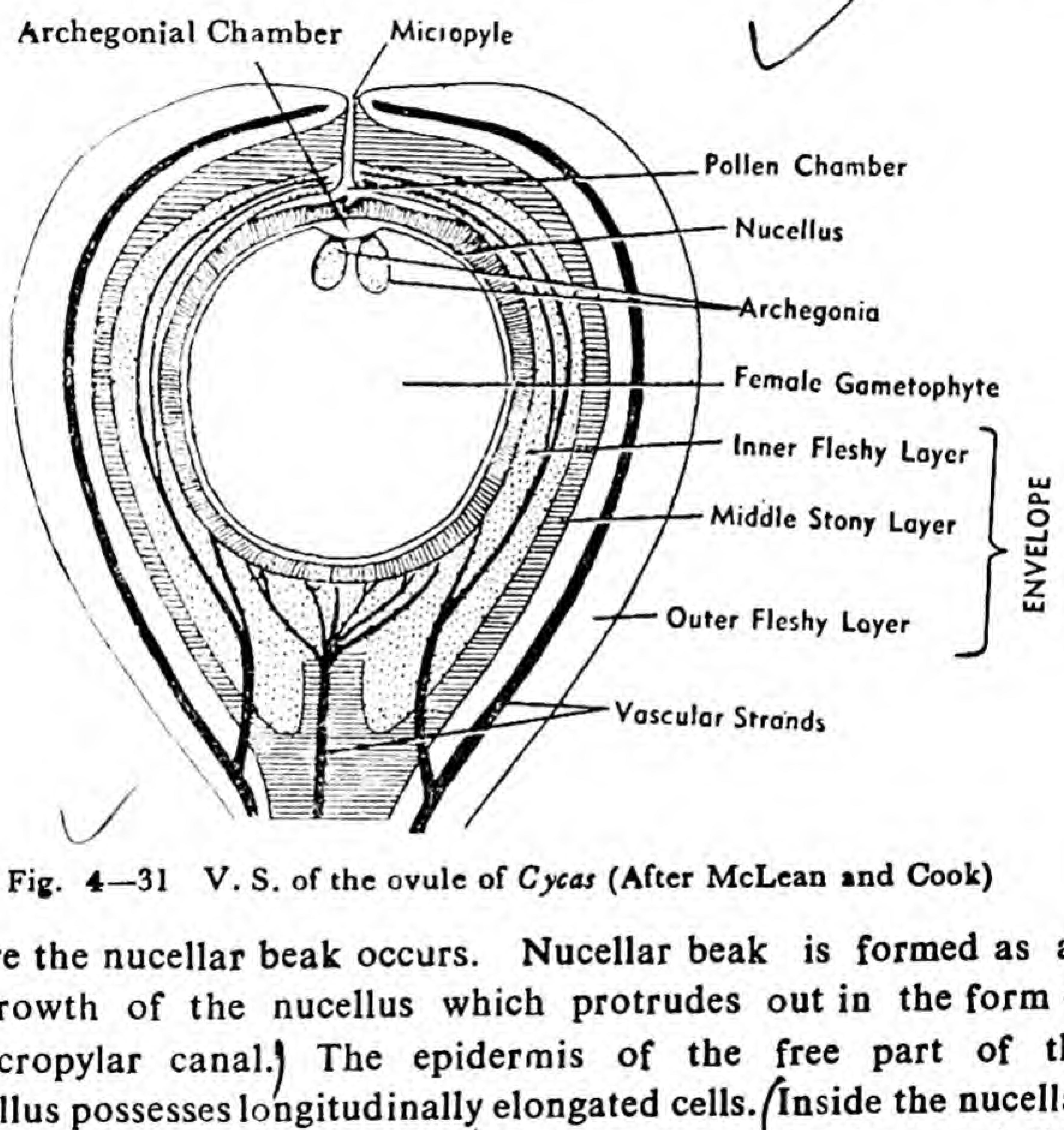



Fig. 4—31 V. S. of the ovule of *Cycas* (After McLean and Cook)

where the nucellar beak occurs. Nucellar beak is formed as an outgrowth of the nucellus which protrudes out in the form of a micropylar canal. The epidermis of the free part of the nucellus possesses longitudinally elongated cells. Inside the nucellar beak occurs the pollen chamber which is formed by the dissolution of the cells of the beak. The ovule is supplied by a pair of vascular bundles at the base, one of which goes to the outer fleshy layer and the other to the inner fleshy layer. These further branch into a dozen vascular bundles (fig. 4-31). The ovule gets considerably enlarged after pollination. Now, a single archesporial cell enlarges and becomes prominent in the upper region of the nucellus; this is the megaspore mother cell. This cell divides meiotically into three

cells in *C. rumphii* in a linear fashion ; the last cell grows at the expense of the neighbouring cells and gradually acquires a large size. The ovule now has nucellus reduced to a thin papery layer and encloses inside a massive female prothallus. Inner fleshy layer also becomes thin but the sarcotesta or the outermost layer remains fleshy till the end.

Fig. 4—32 A young male strobilus of *Cycas circinnalis*.

**Megasporangium (Ovule)**–The largest ovule amongst the living gymnosperms occurs in *Cycas circinnalis*, measuring nearly 6 cm. in length. Sometimes the ovule attains the size of a hen's egg on maturity. The ovule is orthotropous and shortly-stalked. The surface is either smooth or covered with brown hairs as in *C. revoluta*. The ripe ovules are fleshy, bright orange or red in colour.

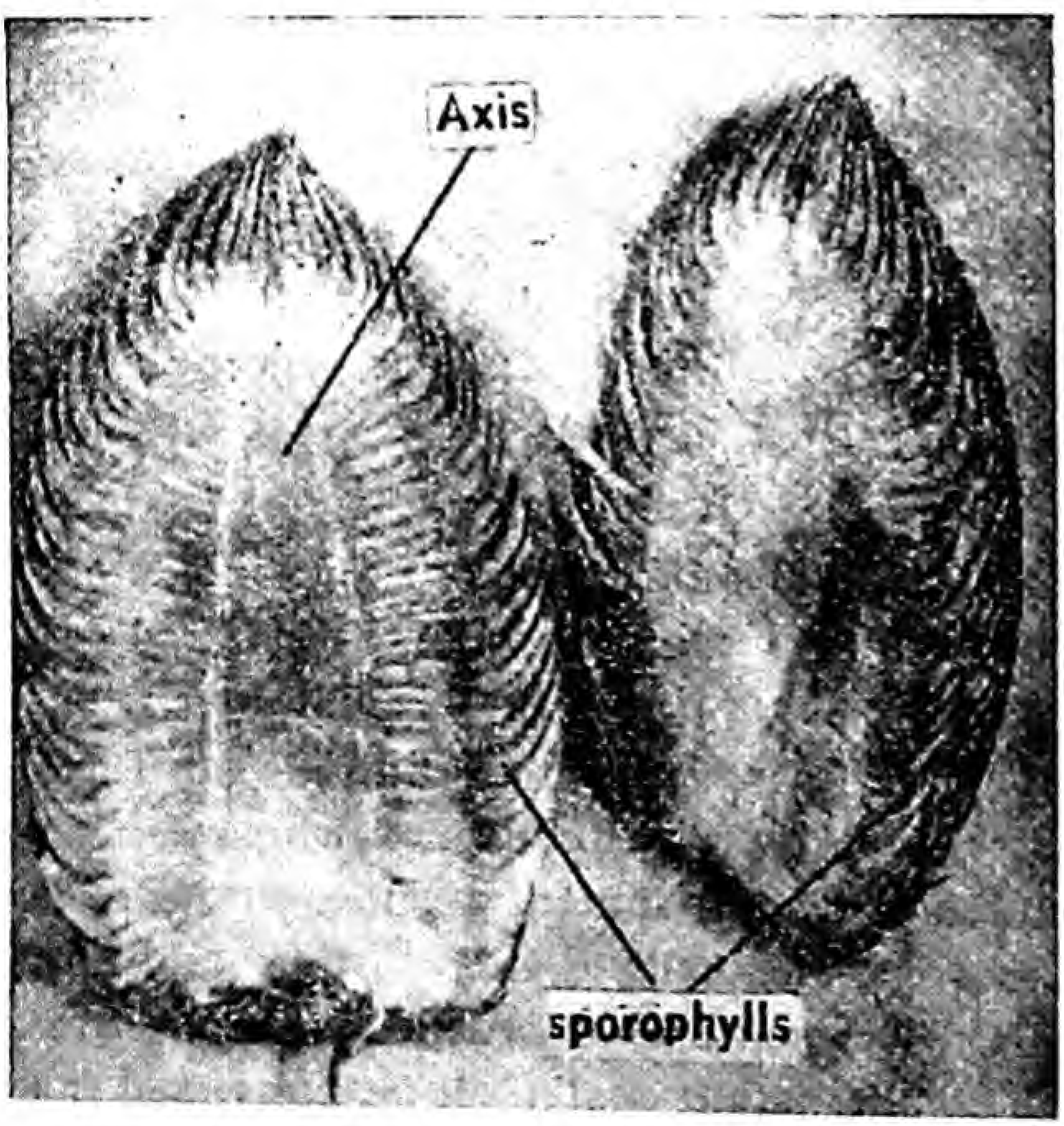



Fig. 4—33 L. S. of a young male strobilus of *Cycas circinnalis*.

**Male strobilus (=Cone)**–It usually develops terminally and is surrounded by a crown of young leaves. Rao's[1] contention

1. Rao, L. N. 1961.

that it is not terminal needs confirmation. The male strobilus is compact and solitary, oval or conical in form and woody in texture (fig. 4-32 & 4-33). Each male strobilus is made up of a number of spirally arranged microsporophylls or stamens. At maturity, in some species of *Cycas*, it may measure up to 50 cm. in length. When microspores or pollen grains are ready for shedding, the axis elongates and sporophylls get separated from one another.

**Microsporophyll**—It arises as a minute outgrowth on the axis. When mature it is flattened and wedge-shaped. The basal narrow part is sterile while the flat distal portion is fertile. In *C. circinnalis* each microsporophyll is 3 to 3.5 cm. long and 1.2 to 2.3 cm. broad. The uppermost sporophylls mature early. Beyond the fertile part of the sporophylls is an upper sterile portion called apophysis (fig. 4-34)

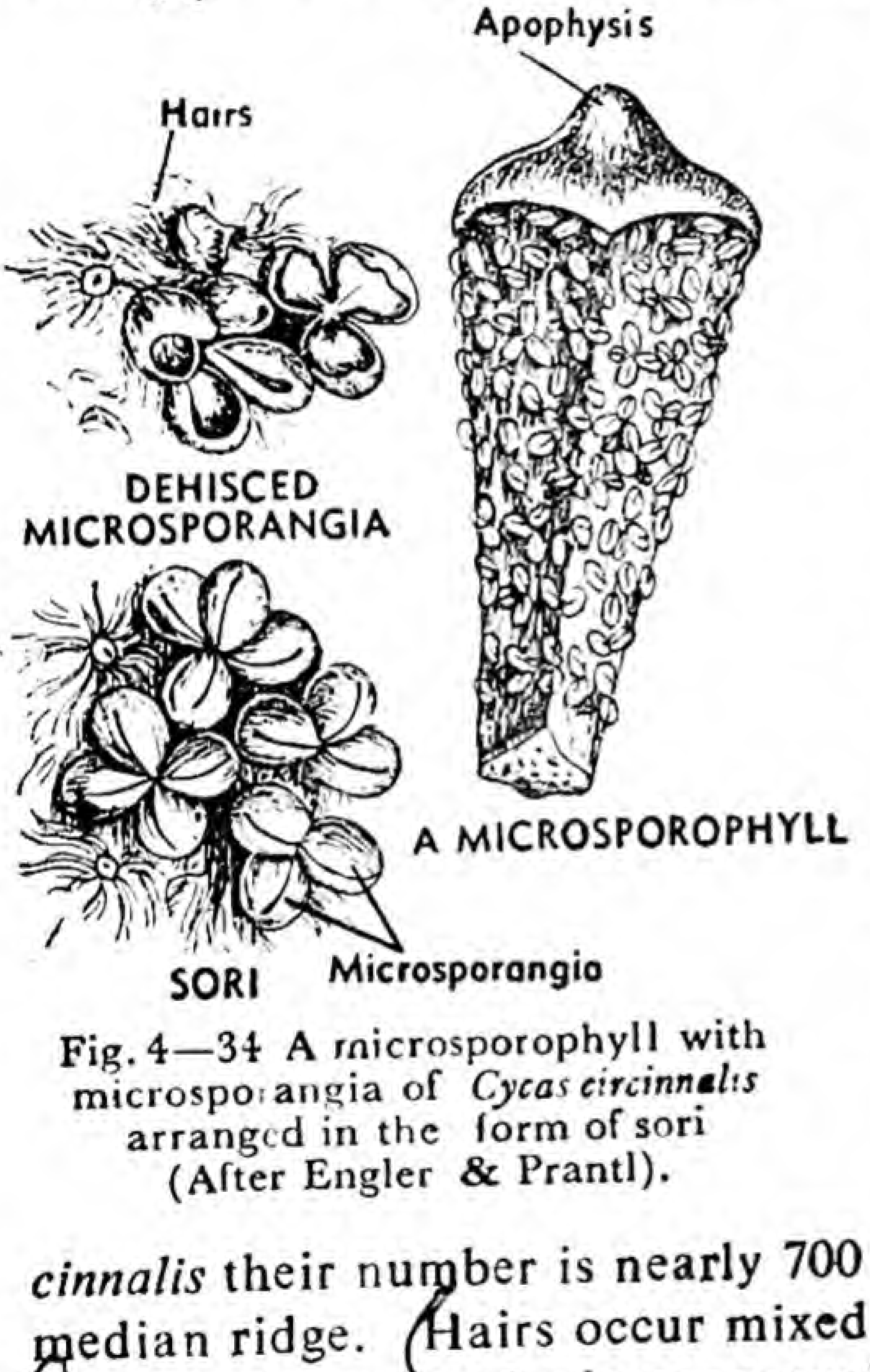


Fig. 4—34 A microsporophyll with microsporangia of *Cycas circinnalis* arranged in the form of sori (After Engler & Prantl).

**Microsporangia**—These are borne on the abaxial (lower) surface of the microsporophyll and are arranged in groups of 3 to 5, in definite sori (fig. 4-34). Each sporophyll is estimated to bear nearly one thousand sporangia. In *C. circinnalis* their number is nearly 700 and they lie on either side of a median ridge. Hairs occur mixed with the sporangia (fig. 4-34). The development of microsporangia is of eusporangiate type, i. e., according to Smith[1], they are formed from a group of superficial initials. These initials divide to form wall cells and primary sporogenous cells. Tapetum, for the nourishment of sporogenous cells, develops later. The sporogenous cells divide further and form microspore mother cells. The mature microsporangia are oval, sac-like structures with a short stout stalk. Rao[2] observed that

1. Smith, F. G. 1907
2. Rao, L. N. 1961

the sporangial wall in *C. circinnalis* is 5 to 6 cells thick and that some of the cells at its anterior end get modified and behave like the annulus of a fern. The sporangium dehisces from this place to release the pollen grains or microspores (fig. 4-35 A to C).

GAMETOPHYTIC GENERATION—The microspore mother cells, formed inside the microsporangia, and megaspore mother cells formed inside the megasporangia (ovules), represent the last stages of the sporophytic generation. Both micro- and megaspore mother cells divide reductionally or meiotically, inside the micro- and megasporangia respectively, producing numerous microspores while only 3 to 4 megaspores, are formed only one of which matures while all the microspores formed are functional. In *C. circinnalis*, Rao[1], and in *C. beddomei*, Shetty and Subramanyam[2] have reported 11 chromosomes in the microspores and 22 in the microspore mother cells. In *Cycas* the megaspores are arranged in a linear fashion. Contrary to the popular notion that 4 megaspores are formed in this genus, DeSilva and Tambiah[3] have shown that in *C. rumphii*, at least, only three megaspores are formed. The megaspore at the base, i.e., farthest from micropyle, ultimately matures, while others degenerate.

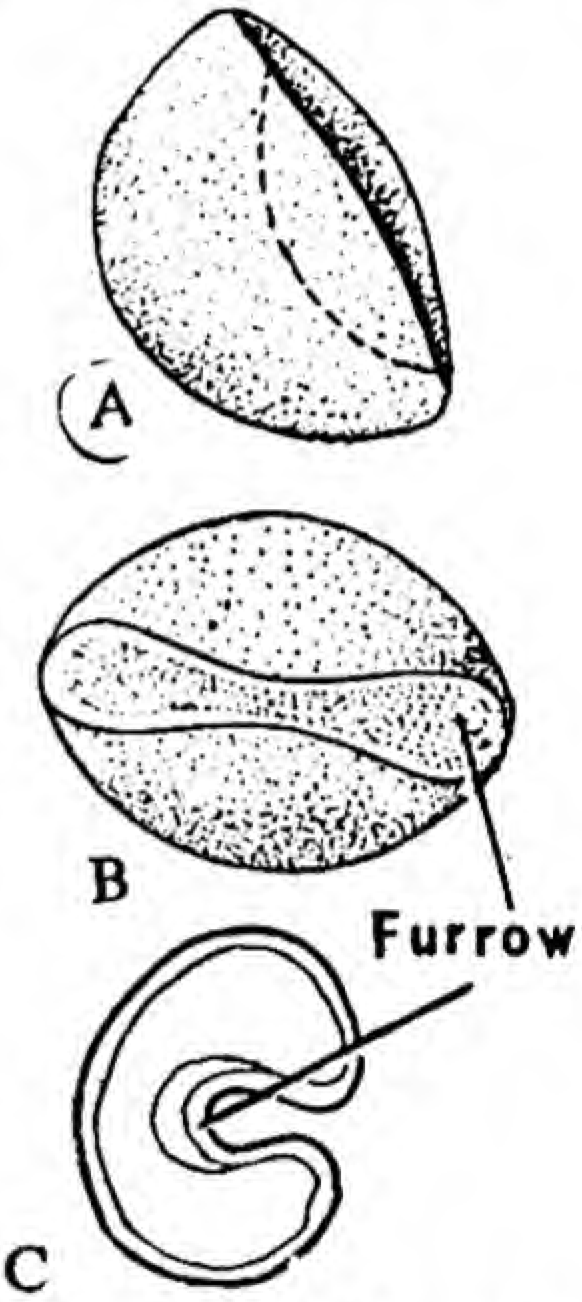



Fig. 4—35 Pollen grains of *Cycas chamberlainii* A–lateral view; B–distal view & C–sectional view (After Wodehouse).

**Female Gametophyte**—Megaspore is the earliest stage of the female gametophyte. It has a thick and papillate outer wall, the exospore and a fibrillar inner one, the endospore. The megaspore divides by free nuclear divisions and a large number of nuclei are formed. A vacuole appears in the centre, which later on gets filled up with a fluid which is like the coconut milk. Cytoplasm collects round the nuclei and cell walls are laid down from the

1. Rao, L. N. 1961.
2. Shetty, B. V. & K. Subramanyam 1962.
3. De Silva, B. L. T. & M. S. Tambiah 1952.

periphery extending towards the centre—centripetal method of cell wall formation. Thus the entire gametophytic tissue becomes cellular, each cell having a single nucleus. This tissue is now called the female gametophyte or endosperm. In the angiosperms the endosperm is formed after fertilization but in *Cycas* it is formed prior to it and also, unlike the former, there is no fusion of any male gamete with the secondary nucleus for its formation. It is thus a haploid tissue in contrast to the angiosperm endosperm which

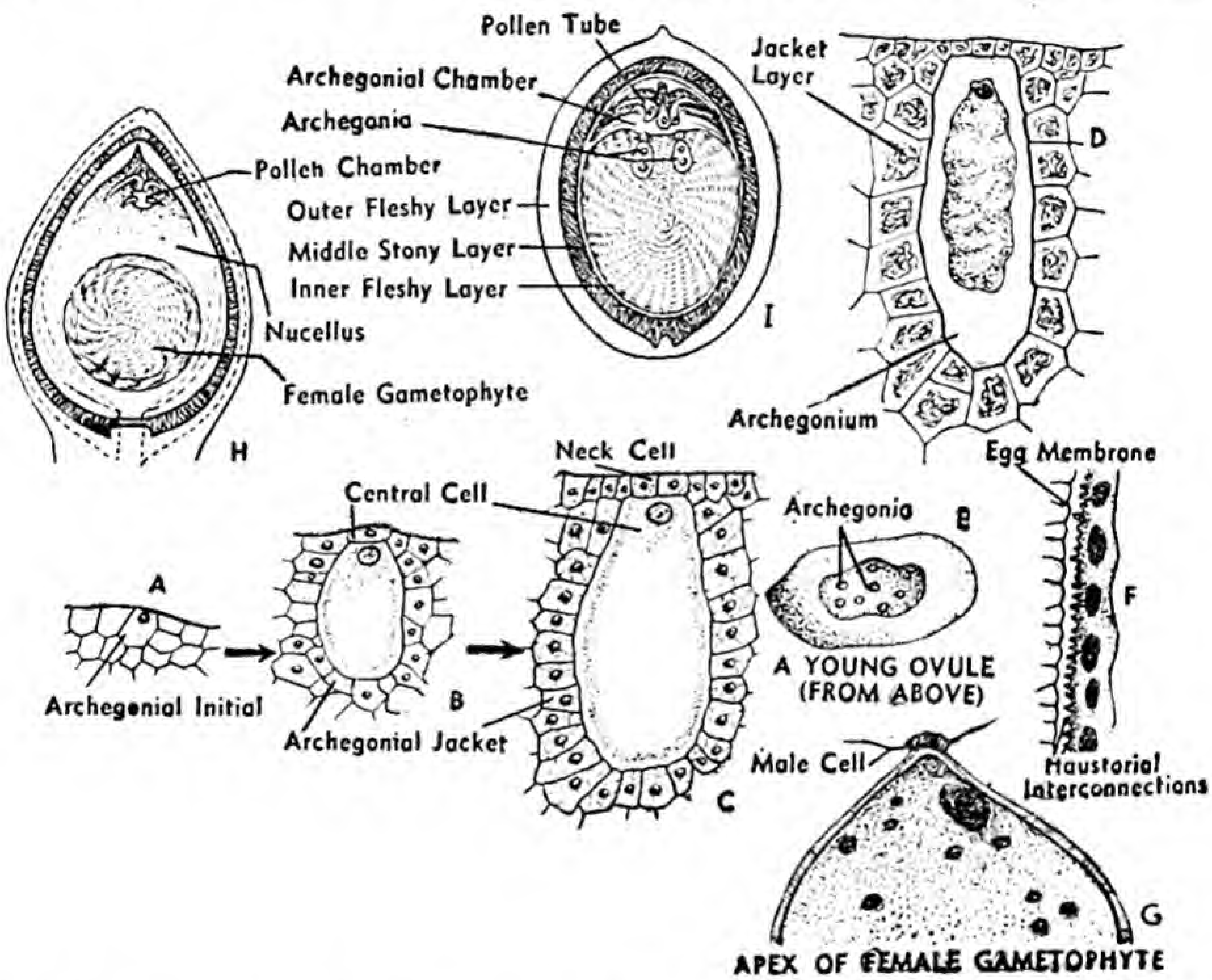



Fig 4—36 Development and structure of the female gametophyte in the cycads. A to C—Development of an archegonium (After Chamberlain); D to G—Details of the structure of the archegonium (After Engler and Prantl); H&I—V. S. of the ovule (After Chamberlain).

is generally triploid and, therefore, it is more appropriate to call it female gametophyte than endosperm. After the formation of the female gametophyte a few cells at the micropylar end enlarge and form the archegonial initials (fig. 4-36 A). The nucellar tissue above these initials disorganises and forms an archegonial chamber (fig. 4-36 I). The archegonial initial divides transversely into a primary neck cell and a central cell; the former

forms the neck and the latter the venter of the archegonium. The neck is made up of only two cells lying side by side (fig. 4-36C). Swamy[1] reports the formation of 4 neck cells in *Cycas sp*. Neck canal cells are not formed in *Cycas*. The central cell forms a ventral canal nucleus and an egg; there is no wall separating the two whereas in *Pinus* a distinct wall is formed. The venter is surrounded by a nutritive jacket of cells called the 'archegonial jacket' (fig. 4-36 B & D). The jacket is formed by the gametophytic cells. The egg of *Cycas* is the largest amongst the living plants. It can be seen with naked eye and measures nearly ½ mm. in diameter in *C. circinnalis*. The number of archegonia may range from 2 to 8 in different species of *Cycas*.

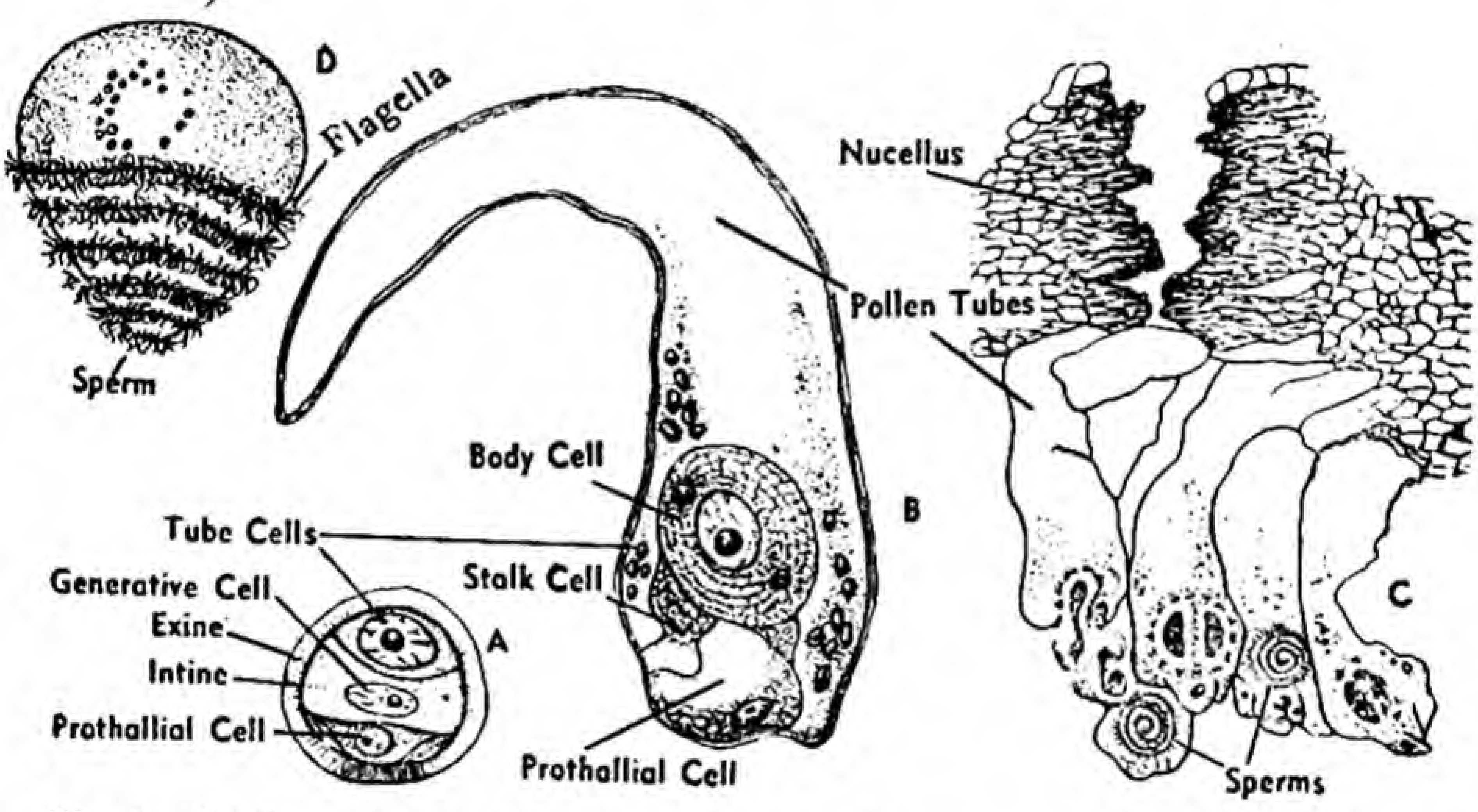



Fig. 4—37 Structure and development of male gametophyte of *Cycas*. A & B—Stages of pollen tube development (After Swamy); C. Pollen tubes developing inside the nucellus (After Swamy); D A. single top-shaped antherozoid with spiral flagellar bands (After Webber).

**Male gametophyte**—The microspore (pollen grain) is boat-shaped in form (fig. 4-35). It has a longitudinal slit and it represents the beginning of the male gametophytic generation. Each microspore is protected by two walls, the outer thicker, exine and the inner thinner, intine (fig. 4-37 A). The microspore germinates while it is still enclosed within the microsporangium. The microspore divides transversely into two unequal cells, a small prothallial

1. Swamy, B. G. L. 1948.

cell and a large antheridial cell. The latter divides and produces a generative cell and a tube cell. The tube cell possesses a comparatively larger nucleus than the generative cell. Microspore or pollen grain is shed at this three-celled stage (fig. 4-37A). De Silva and Tambiah[1] state that the microspores in *C. rumphii* are shed in April while Pilger[2] found that they were shed in June-July in *C. revoluta*.

**Pollination**—In *Cycas* the pollination is anemophilous. The microspores are carried to pollen chamber of the ovule by wind. When the archegonium matures a mucilaginous pollination drop exudes out of the micropyle. To this drop, a large number of microspores floating in the air, get attached. With the drying up of this drop pollen grains get sucked inside the pollen chamber. The microspores in *Cycas revoluta* lie inert inside the pollen chamber for nearly four months before germinating (fig. 4-37C).

Holttum states that in *C. rumphii* and *C. siamensis* (the two species that occur in Malaya) there is a very penetrating odour when either young leaves or reproductive organs (male or female) start maturing. It is strongest in case of male strobili before the pollen grains are ripe. It has been confirmed by us in the case of *Cycas circinnalis*. This odour probably has nothing to do with the pollination mechanism.

**Post-pollination changes in the male gametophyte**—After the microspore has remained inside the pollen chamber for almost 4 months the generative cell divides into a sterile (stalk) cell and a spermatogenous[3] (= body) cell (fig. 4-37B). Pollen tube then elongates and grows into the tissue of the nucellus acting both as a haustorium as well as a sperm carrier (fig. 4-37C). The spermatogenous or the body cell increases in size and two blepharoplasts make their appearance near the nucleus. The spermatogenous (= body) cell ultimately divides into two sperm mother cells, each of which possesses a blepharoplast. Finally the blepharoplast forms a large spirally arranged structure on which a large number of flagella arise. The

1. De Silva, B. L. T. & M. S. Tambiah 1952.
2. Pilger, R. 1926.
3. Sterling, C. 1963.

antherozoid or sperm is now top-shaped and fully formed (fig. 4-37D). The two sperms thus formed swim freely inside the pollen tube and show a rotational movement. They swim with their broad ends downwards. In *Zamia integrifolia* Pursh. ( = *Zamia floridanna* var *purshiana* Schuster), it has been shown by Nostog and Overstreet[1] that the movement of sperm involves two kinds of flagellar actions, namely (i) a vibrating movement of individual flagella and (ii) a periodic roving movement of entire flagellar complex. Besides the flagellar movements the sperms also show amoeboid movement while coming out of the pollen tube. The size of sperms varies from 180μ to 210μ in *C. revoluta* and *C. circinnalis*.

**Fertilization**—The pollen tube, acting as a haustorium is turgid in nature. It penetrates the nucellar bridge; later it bursts releasing the two sperms, and becoming flaccid. Swamy[2] states that an aperture is formed at the apex of the pollen tube for the release of the sperms. The rupture of pollen tube also releases a fluid of high osmotic concentration. As soon as a sperm touches the neck cells of an archegonium it is violently sucked in, thus a single sperm reaches near the egg nucleus (fig. 4-38A). Swamy[2] states that many sperms may sometimes reach the cytoplasm of the egg but only one of them fertilizes it. The egg nucleus is much larger in size than the sperm nucleus. The male and female nuclei later fuse together to form a zygote (fig. 4-38D & E). Thus in *Cycas* the sperms are carried to the

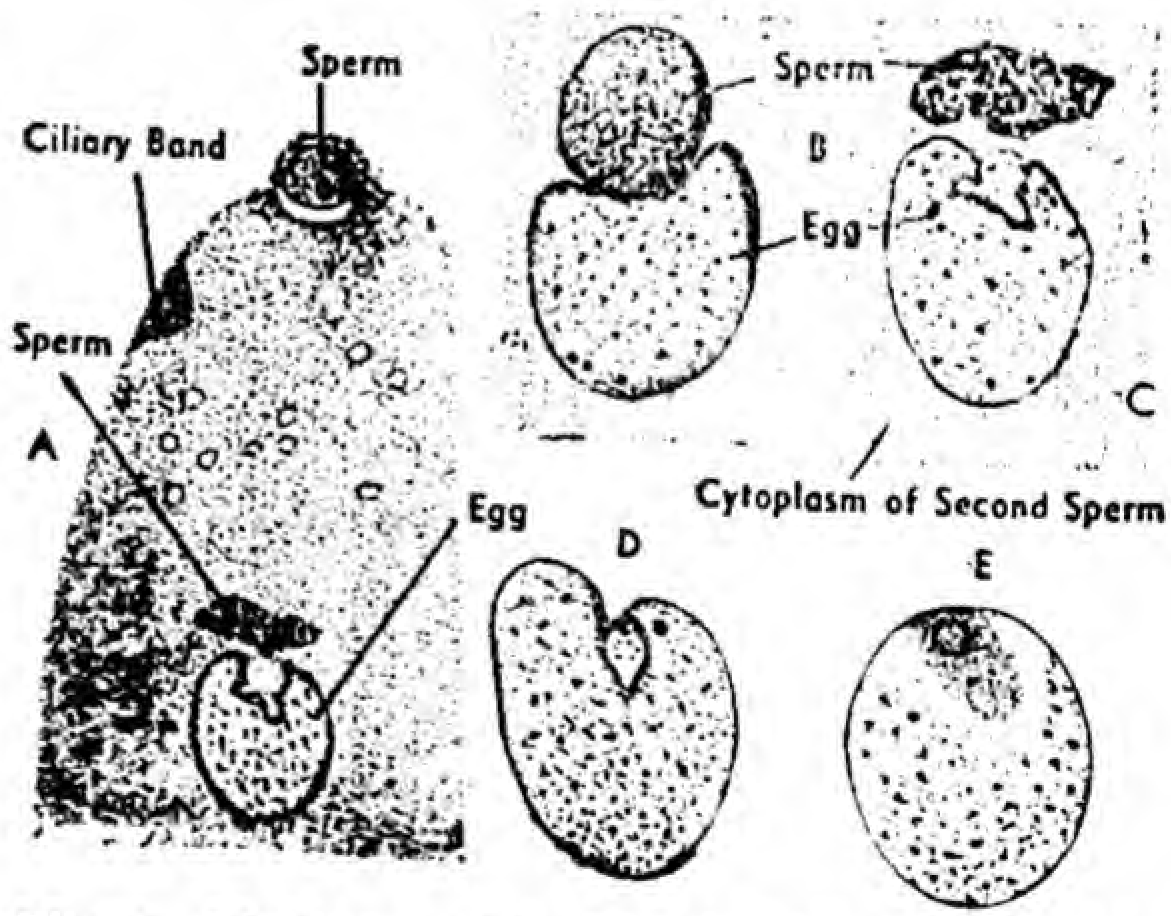


Fig. 4—38 Stages of fertilization in *Cycas revoluta* (After Wettstein). A to C—Preliminary stages; D & E—stages of gametic fusion.

1. Nostog, K. & Rose Overstreet 1965.
2 Swamy, B. G. L. 1948.

egg in the pollen tube. Such a process is termed 'siphonogamy'; it is also accompanied by 'zoodiogamy' (the sperms are motile). Engler[1] & Prantl keep gymnosperms and angiosperms together under one taxon—'Embryophyta Siphonogama', because of the presence of a pollen tube in both the taxa.

**Apomixis**—This phenomenon has been reported in *Zamia floridana* A. DC. and *Cycas revoluta* Thunb. La Rue[2&3] has demonstrated it in vitro cultures of the female gametophytes. The miniature plants, thus produced, were haploid, hence he inferred that one generation of life-cycle can be reproduced from the other by direct regeneration from the tissue without sexual intervention.

DEVELOPMENT OF THE SPOROPHYTE—The zygote ~~in *C. circinalis*~~ may be 2 to 3 mm. long with its nucleus being 0.8 to 1.0 mm. in diameter[4] It divides by free-nuclear divisions. Such divisions result in the formation of 200 to 300 nuclei. ~~In *C. circinalis*, however, the number of nuclei formed is more than 128 but never 256.~~[4] Simultaneously a vacuole develops in the centre of the zygote and the nuclei thus get pushed to the periphery. There are more nuclei at the lower end of the embryo than at

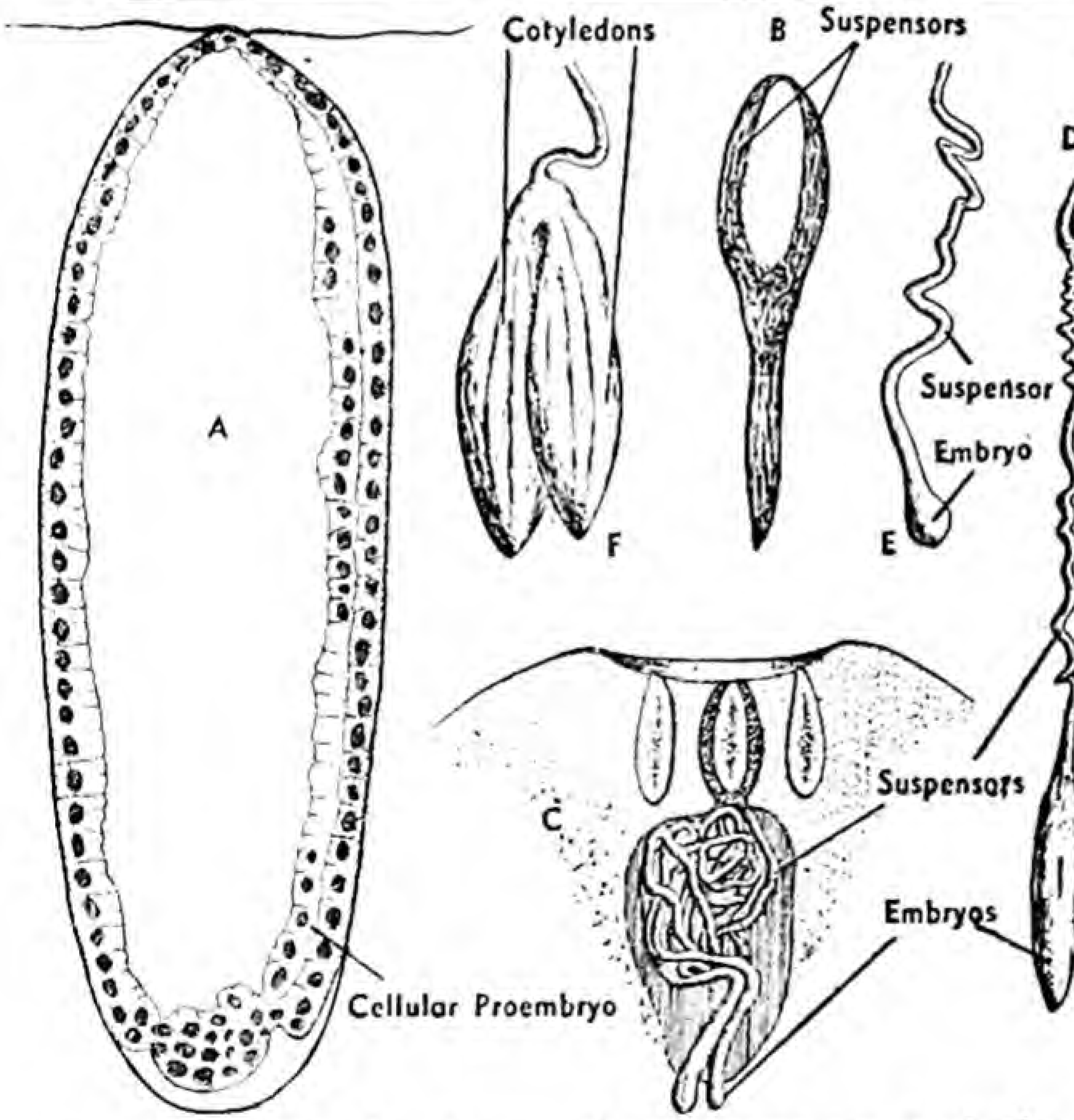



Fig. 4—39 Early stages of embryogeny and the development of embryo in *Cycas circinnalis* (After Engler and Prantl). A–Young proembryo; B–Young embryo with two suspensors; C—L. S. of the seed with two embryos; D & E—Embryos with long and coiled suspensors; F—An embryo with two fully developed cotyledons.

1. Engler, A. & K. Prantl 1889.
2. La Rue, C. D. 1948.
3. " 1950.
4. Rao, L. N. 1963.

the micropylar end. Wall formation starts from the periphery to the centre of the embryo, i. e., the cell wall formation is centripetal. After the walls have been laid down, this stage of the embryo is called the 'proembryo stage' (~~fig. 4-39 A~~). The proembryo gets differentiated into three regions ; the uppermost region near the micropyle is called the haustorial region, the middle one the suspensor and the lowermost the embryonal region. Several archegonia in an ovule may get fertilized and several embryos along with their suspensors may be formed but only one embryo matures ultimately. The suspensor elongates rapidly and pushes the embryonal region deep into the endosperm. Rapid elongation of the suspensors results in their getting much coiled and twisted (~~fig. 4-39C&D~~). The suspensor of the successful embryo is made up of the coiled suspensors of all the embryos in an ovule (~~fig 4-39D~~). The embryo takes about an year for its full development. This may happen while the seed is still attached to the plant or the maturation may be completed after the seed has fallen to the ground. Coleorhiza which partly develops from the suspensor is the first to make its appearance at the micropylar end of the embryo. It becomes hard on maturity. At the basal end of the embryonal region develops a cylindrical stem apex, the two cotyledons in the form of minute protuberances arising laterally. Later the cotyledons enlarge and enclose the stem apex in between them (~~fig 4-39F~~). Root in the form of the radicle develops quite late. Th~~e mature embryo is straight and the hypocotyl is qu~~ite ~~small. The first leaves are~~ decussate ; they arise at right angles to the cotyledons. Schuster[1] in a few abnormal embryos of *C. circinnalis* found ~~one or three cotyledons. He also~~ records ~~instances of unequal cotyledons in *C. circinnalis* L~~inn. ( = *C. madagascariensis* Miq.) As the megasporangium is fully covered over by an envelope, and as the gametophyte does not protude out of it, this structure is regarded as a true seed.

**Structure of seed.**—The mature seed of *Cycas* is fleshy, red, orange or brown in colour. It is enclosed by a thick coat called the testa which is formed from the outer layer of the envelope which

1. Schuster, J. 1932.

now becomes soft. ~~According to Rao[1]~~, it has a sweet taste and pleasant odour. This attracts birds and animals which help in the dispersal of the seed. Inside the testa, shrivelled nucellus, endosperm and a straight embryo are present.

Pant and Nautiyal[2] observed seven different membranes in the seeds of *C. beddomei*, *C. circinnalis*, *C. pectinata* and *C. revoluta*. Two of these surround the envelope on the outer and inner sides, a third one shows the impressions of the vascular strands, the fourth covers the nucellar cap and the rest three surround the megaspore, the egg and the embryo respectively.

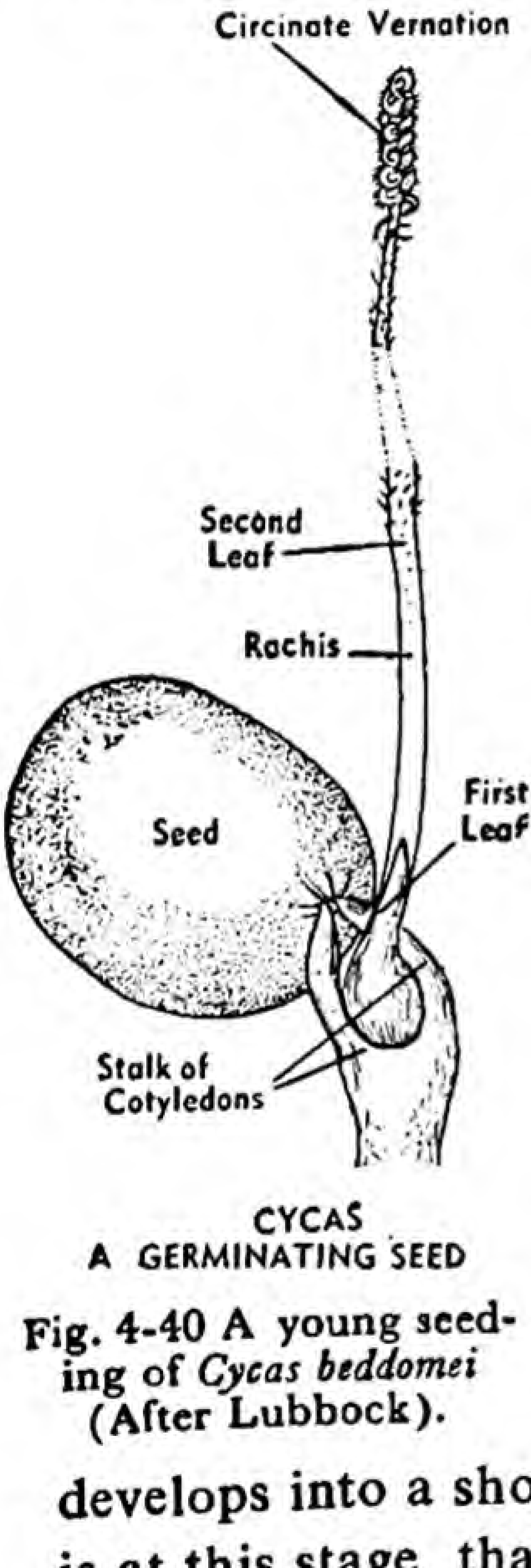



Fig. 4-40 A young seeding of *Cycas beddomei* (After Lubbock).

The seed falls to the ground and needs some resting period for germination into a seedling. ~~De Silva and Tambiah[2] state: "There is a further period of physiological immaturity as the seeds do not germinate for a long time even after~~ the embryo is fully formed". The cotyledons do not come out of the seed during germination, as they are haustorial in nature, but their bases remain exposed, hence the seed germination may be said to be epigeal ~~(fig. 4-40)~~. The radicle after piercing the coleorhiza emerges out of the micropyle to form the primary root; the plumule develops into a shoot, later forming a pinnately divided leaf. It is at this stage that lateral rootlets arise from the hypocotyl. They become swollen and develop into coralloid roots. ~~The young leaf shows circinate vernation (fig. 4-40). Now the coleorhiza dries and becomes papery. Usually several weeks pass before the first leaf emerges.~~ The first crown of leaves is borne after several years of growth of the plant.

1. Rao, L. N. 1963.
2. Pant, D. D. & Nautiyal 1953.

**Stages in fertilization and seed maturation**—De Silva and Tambiah[1] studied the life-history of *C. rumphii* and observed that it takes 3 years for its completion. The different stages as noticed by them are summarized below :

**First Year**

Visibility of male strobili and tips of megasporophylls. Development of ovule and the formation of female gametophyte ..... —March

Maturation of male strobili and megasporophylls.—April-May.

Pollination and the pollen tube formation. —May.

Division of generative cell into a sterile cell and a spermatogenous cell. —July.

**Second Year**

Breaking up of the floor of pollen chamber. —March

Rotation of blepharoplasts. —December.

Spermatozoid formation and fertilization. —June.

Embryo development. —November.

**Third Year**

Dropping of seed from mother plant. —January.

Differentiation of cotyledons. —March.

ECONOMIC IMPORTANCE—Apart from its ornamental value for which *Cycas* is planted in gardens, it is cultivated extensively in Japan as a source of 'sago' which is prepared in the following ways :—

After the removal of the bark the trunk is cut into thin discs, which are then dried and finally ground. Later, a thick paste with water is made. Excess of water is now added and it is then allowed to stand. The starch settles down and the clear upper fluid is drained off. The starch in the form of paste is rolled between boards which give it a characteristic round shape. It is then dried and sold in the market as 'sago'.

1. DeSilva, B. L. T. & M. S. Tambiah, 1952.

Hill[1] states that the starch paste is passed through sieves, which give the round shape to the pellets. These are then dried and sold in the market under the name 'sago'.

Sago can also be obtained from the seeds which contain about 31% starch besides some harmful glucosides, which can be removed by repeated washing with water[2]. The flour of seeds is termed 'Indum podi' in South Malabar and is used in the preparation of cakes and porridges. Seed-kernel is also of food value. In Assam, Malaya, Indonesia, etc., the young succulent leaves are cooked as vegetables. *C. rumphii* yields a kind of gum.

RESEMBLANCES WITH OTHER GYMNOSPERMS—*Cycas* like most gymnosperms possesses, conjoint, collateral and open vascular bundles. The phloem has no companion cells and the xylem has no vessels. The female gametophyte is reduced and is retained within the sporophyte. It is also completely dependent on it. The sporophylls are aggregated through, only in the male strobilus. Pollen tube develops inside the pollen chamber. Archegonia have no neck canal cells. Neck is reduced. Proembryo is formed and the suspensor is formed for helping the proembryo to obtain nourishment during its development. Endosperm develops before fertilization.

RESEMBLANCES WITH THE FILICINEAE (FERNS)-*Cycas* in its structure and life-history retains certain primitive characters, these are similar to those of ferns. Stem in the young stage is underground and subterranean. Leaf-bases, similar to tree ferns are present. Young leaves are circinately coiled. Sporophylls are leaf-like. Sori are present on abaxial or lower surface of the microsporophylls. Development of microsporangia is eusporangiate. The output of microspores (pollen grains) is enormous. Sperms are multiflagellate and motile and fluid is still essential for fertilization.

1. Hill, A. F. 1951.
2. Wealth of India 1950 : 409-410.

Chapter 5

# Ginkgoales

The ginkgoales include two families, the Ginkgoaceae and the Trichopityaceae. The only living species *Ginkgo biloba* Linn. is represented by five varieties[1] viz., *G.biloba* var. *aurea* (Nelson) Beisson, *G. biloba* var. *fastigata* Henry, *G. biloba* var. *laciniata* Carriére, *G. biloba* var. *pendula* Carriére and *G. biloba* var. *variegata* Carriére.

The Ginkgoales originated in the Palaeozoic and had a world-wide distribution in the Jurassic. Leaf genera like *Ginkgoites* Seward and *Baiera* Braun have been collected from the upper Gondwanas of India. The most common species of the genera occurring in India were *Baiera indica* Lele, *Ginkgoites crassipes* Feistm., *G. lobata* Feistm. and *G. feistmantelli* Bose & Sukhdev.

The only living species is mostly confined to the eastern part of China and Japan and is planted near temples by priests in these countries. The *Ginkgo* plant is also widely cultivated in the gardens in Europe and America. In India a few cultivated trees are found in the hills. Because of the presence of a number of primitive characters and because of its long geological record, *Ginkgo* is sometimes called a 'living fossil'.

DISTINGUISHING FEATURES—The order is characterized by the presence of large trees possessing dimorphic shoots. Wood is compact and pycnoxylic resembling that of the conifers. Leaves are large and leathery, they are deeply divided and have dichotomous venation. The male strobili are axillary in position. They are unbranched, catkin-like, with a main axis and lateral stamens or microsporangiophores. Each microsporangiophore bears 2-12 pendant microsporangia. The female reproductive organs or ovules are borne on peduncles arising in the axils of leaves. The peduncle bears usually 2 but rarely up to 10 terminal ovules. Male gametes are motile and have spiral flagellar bands as in *Cycas*. Seeds are large; they have an outer and inner fleshy and the middle stony layers which are derived from the ovular envelope

1. Dallimore, W. & A. B. Jackson 1948.

CLASSIFICATION—The order has been divided into two families, viz., the Trichopityaceae and the Ginkgoaceae Engler[1]. The former includes a single fossil genus *Trichopitys* Saporta while the latter includes seven genera namely, *Sphenobaiera* Florin, *Ginkgoities* Seward, *Bairera* Braun., *Arctobaiera* Florin, *Windwardia* Florin, *Eretmophyllum* Thomas and *Ginkgo* Linn.

## *GINKGO* Linn.

SYSTEMATIC POSITION—

Order—*Ginkgoales*

Family—*Ginkgoaceae*

Genus—*Ginkgo* Linn.

MORPHOLOGICAL FEATURES—*Ginkgo biloba* commonly called the 'Maiden-hair tree', is a tall and branched tree

Fig. 5—1 Habit of *Ginkgo biloba* (After Wilson & Loomis).

cultivated for its edible seeds and is also grown as an ornamental plant (fig. 5-1). The branches are dimorphic, i. e., long and dwarf

1. Sporne 1965 : 165.

(spur) shoots occur as in *Pinus*. The long shoots elongate rapidly while the dwarf shoots grow rather slowly. The dwarf shoots possess a crown of leaves above and leaf-scars below. These, because of their active growth, may develop into long shoots or the long shoots may remain dwarf. *Ginkgo* trees possess a long tap root which penetrates deep into the soil.

The leaves of *Ginkgo biloba* are petiolate and large while the scale leaves are small. The foliage or photosynthetic leaves are highly variable in shape. For instance, leaves on dwarf shoots or spurs may be more or less entire like those of the fern *Adiantum*, while the leaves which arise on the long shoots are deeply lobed and generally split into two, hence the specific name *'biloba'* (fig. 5-2). Leaves which arise at the apex or on the long shoots of the first year or of the seedlings are more deeply lobed and may also possess secondary lobes. Venation of the leaves is dichotomous (fig.5-2). Leaves are shed in autumn and prior to shedding their colour turns golden-yellow.

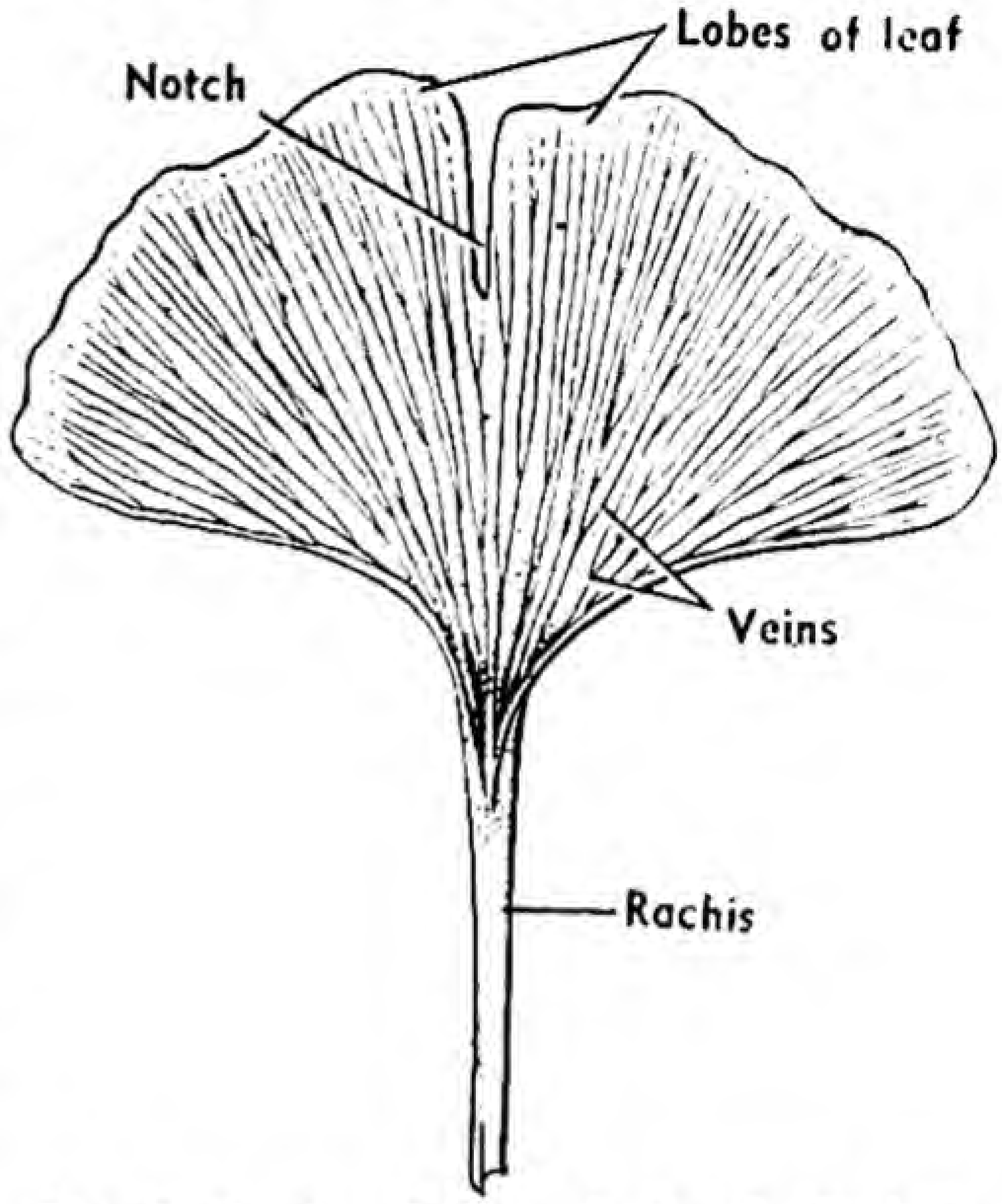


Fig. 5—2 A foliage leaf of *Ginkgo biloba* showing an apical notch and venation.

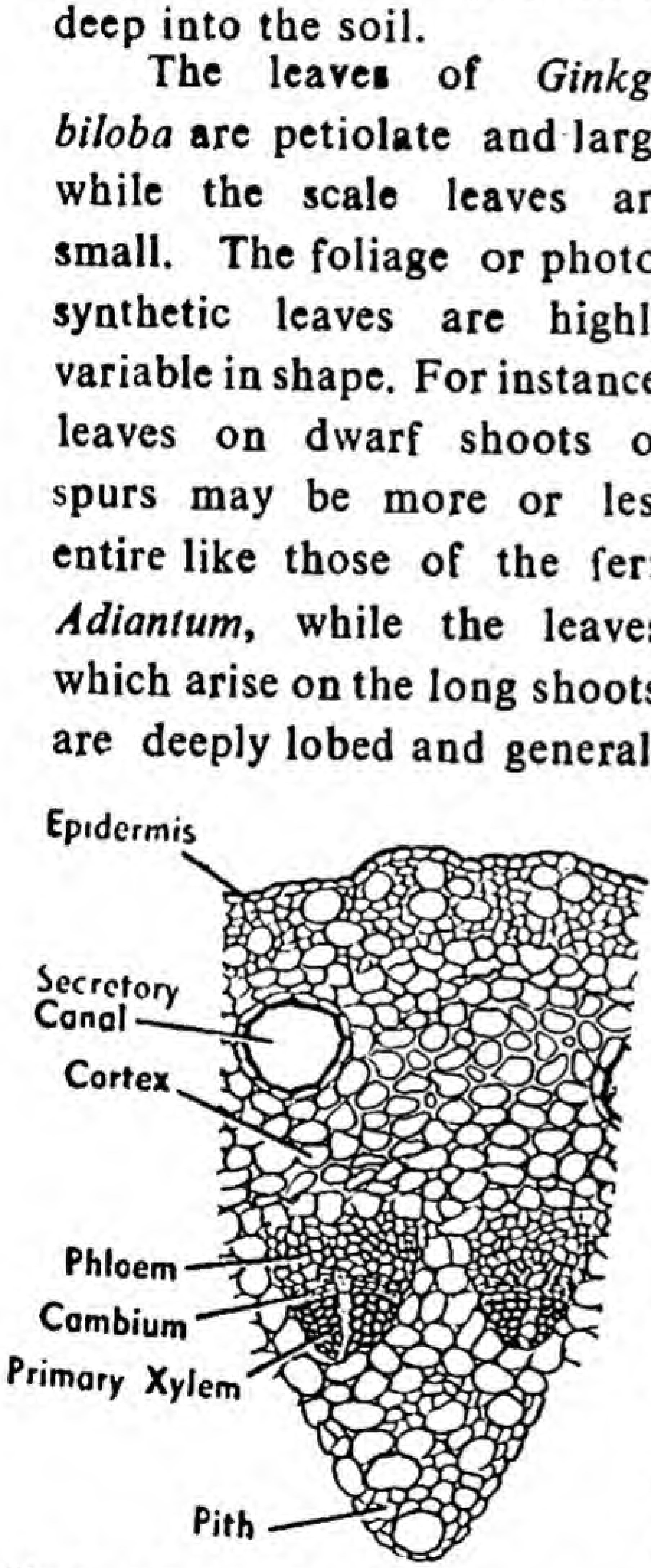


Fig. 5—3 T. S. of a young dwarf shoot of *Ginkgo biloba* with secretory canals in the cortex and a ring of vascular bundles around the pith.

HISTOLOGICAL FEATURES—The stem of *Ginkgo* possesses small centrally situated pith, surrounded by a ring of endarch strands forming siphonostelic vascular cylinder (fig. 5-3 & 4). Mucilage

( =secretory) canals, tannin cells and crystals of calcium oxalate occur widely distributed in the pith as well as in the cortex.

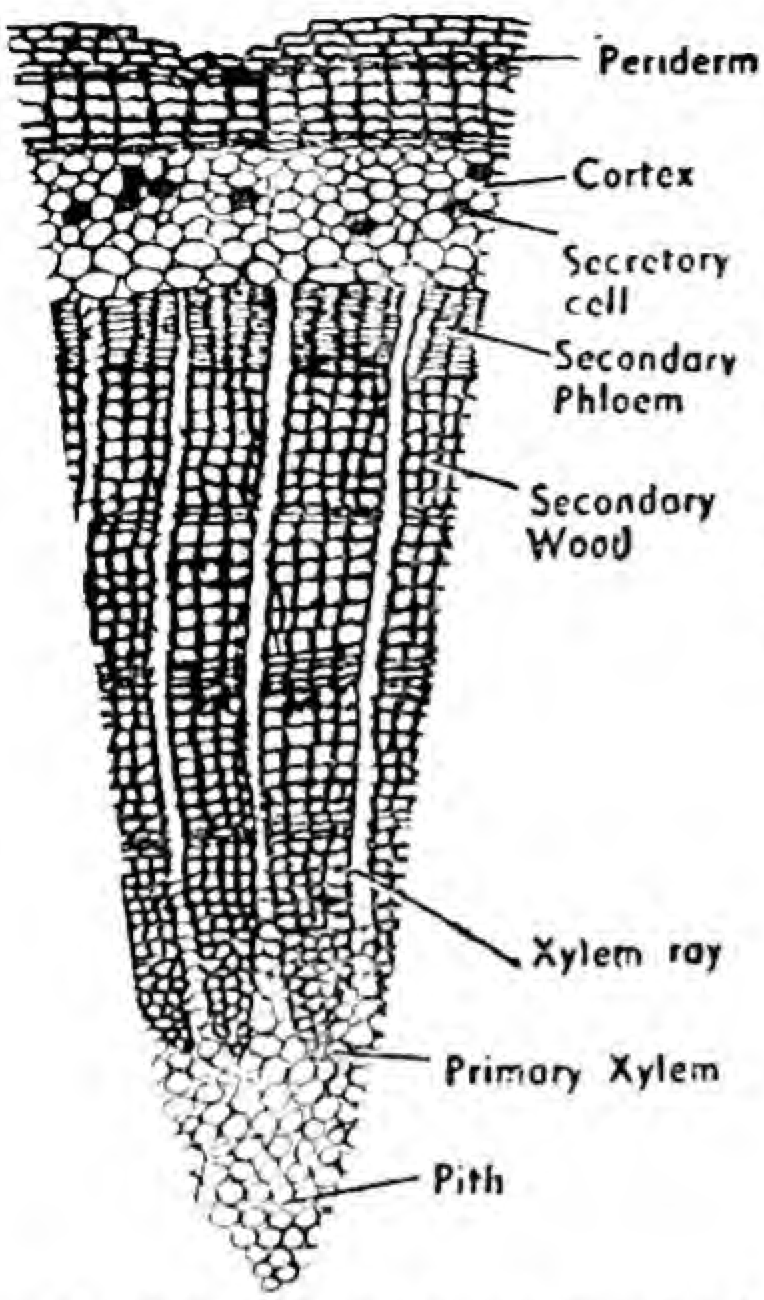



Fig. 5—4 T. S. of a long shoot of *Ginkgo bil ba* with secondary growth.

The tracheids of secondary wood possess one or two rows of bordered pits on their radial walls. In between the bordered pits occur the crassulae and trabeculae which cross the lumen of the tracheid. The long and dwarf shoots differ histologically from one another in the following details :

The long shoot has less of pith and cortex, the secondary wood is harder and more developed (fig. 5-4 and the xylem rays are shorter (fig. 5-5). The dwarf shoot, on the other hand, has a greater development of pith and cortex and has many more mucilage canals (fig. 5-3).

The veins of *Ginko* leaf are accompanied by a small number of reticulate transfusion tracheids. Distally the water conducting elements may be replaced by a few short pitted tracheids. The vascular bundle of the vein is endarch, it has a few large cells filled with brown contents both below and above it (fig. 5-6). Stomata, sunken in pits, are distributed on both the surfaces of the leaf[1]. The petiole is supplied with a pair of endarch vascular bundles.

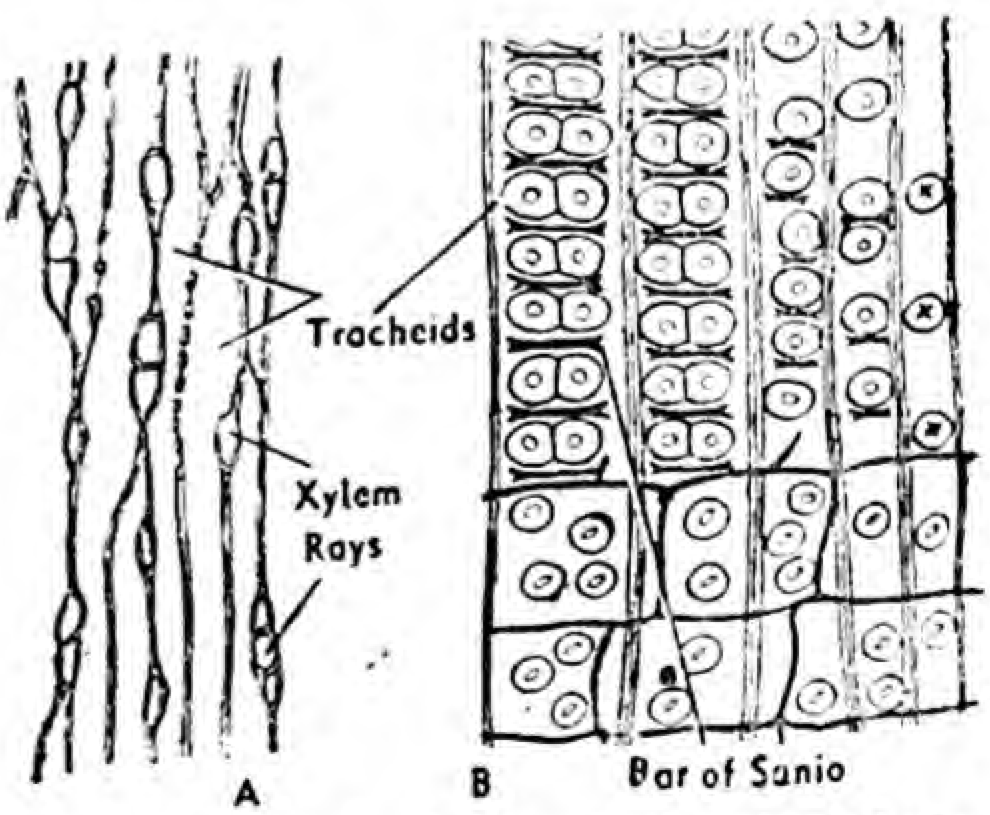



Fig. 5—5 T. L. S. of the secondary wood of *Ginkgo biloba* with xylem rays.

The root of *Ginkgo* is usually diarch, but sometimes it may be triarch. Tannin and starch occur in abundance within the

1. Kanis, A. &. W. K. H. Karstens 1963.

parenchymatous cells. Endodermis is distinct in the beginning but may not remain so at maturity. The mature roots have annual rings.

## LIFE-HISTORY

The trees of *Ginkgo* are dioecious. The male and the female strobili occur on different plants and they are in many ways quite primitive.

**Male reproductive organs**—The male strobili of *Ginkgo* arise on the dwarf shoots (fig. 5-7). It consists of a central axis surrounded by a large number of spirally arranged microsporophylls or microsporangiophores. Each microsporophyll bears a 'hump' containing a mucilage sac and two pendant microsporangia. The development of microsporangia is of eusporangiate type. The sporogenous cells by repeated divisions form the microspore mother cells; these divide meiotically to form spores or pollen grains. Microsporangia dehisce through a longitudinal slit.

Fig. 5—6. T.S. of a leaf vein of *Ginkgo biloba* (After Seward).

**Female reproductive organs**—From the axils of the scale leaves arise long stalks or peduncles which bifurcate apically. Each bifurcation usually bears a single ovule or megasporangium. Out of the two sessile ovules, borne on a peduncle, one may abort earlier. Rarely there may be 3, 4, or more ovules on each peduncle. It was at one time thought that each ovule had probably arisen on a megasporophyll, and that several megasporophylls fuse together at the base to form the peduncle. Propounders of this

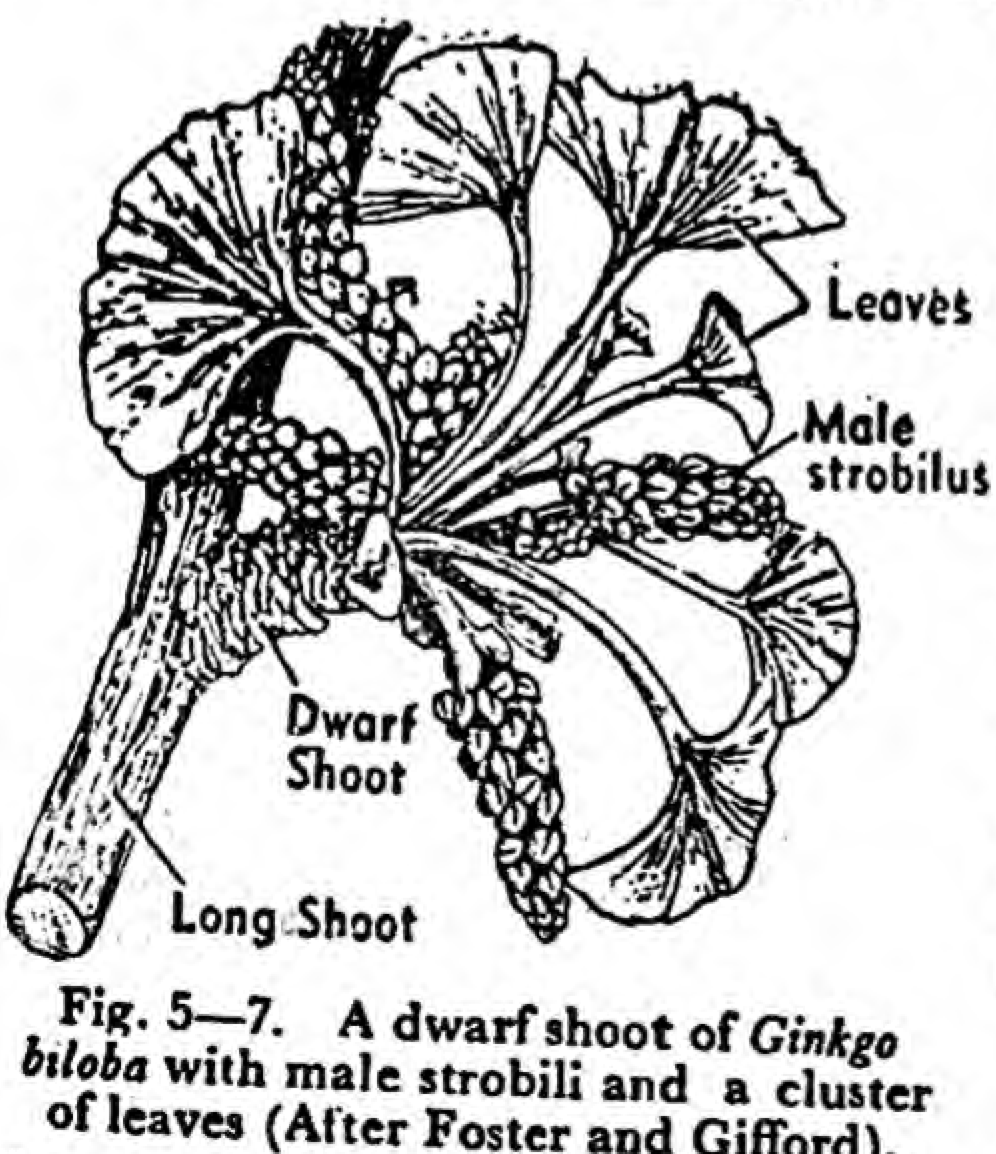


Fig. 5—7. A dwarf shoot of *Ginkgo biloba* with male strobili and a cluster of leaves (After Foster and Gifford).

view regarded the collar (fig. 5-11D), a structure that surrounds the ovule, as a modified lamina. This theory of foliar nature of peduncle has recently been discarded. It is now believed that the peduncle is a modified shoot which bears ovules at its apex.

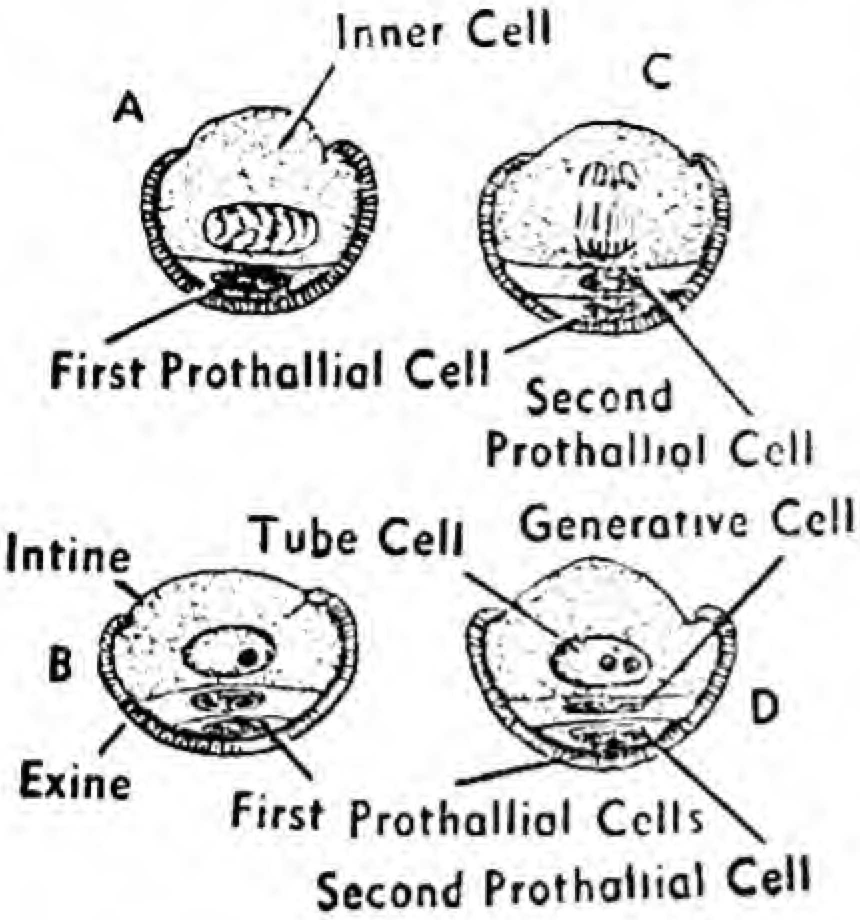



Fig. 5—8 Early stages of the development of male gametophyte of *Ginkgo biloba* (After Chamberlain) A—a pollen grain with incomplete exine, first prothallial cell and inner cell; B—a pollen grain with first and second prothallial cells; C—a pollen grain with prothallial cells and dividing antheridial initial; D—A pollen grain at the shedding stage with two prothallial cells, generative cell and tube cell, first prothallial cell is aborting.

The ovules, during their development, break through the bud scales and pollination may take place while the ovules are immature. Each ovule is surrounded by a three-layered envelope similar to that of *Cycas*. Megaspore mother cells become prominent in the nucellus; they divide meiotically to form four megaspores arranged in a linear fashion. Out of the 4 megaspores usually the lowermost one or rarely two, are functional. Cells at the apex of the nucellus form a conspicuous structure called 'tent pole' (fig. 5-11B). The nucellar beak and pollen chamber are like that of *Cycas*. Ovules are surrounded by a collar (fig. 5-11D). A pollination drop exudes out of the micropyle to catch the pollen grains which are floating in the air.

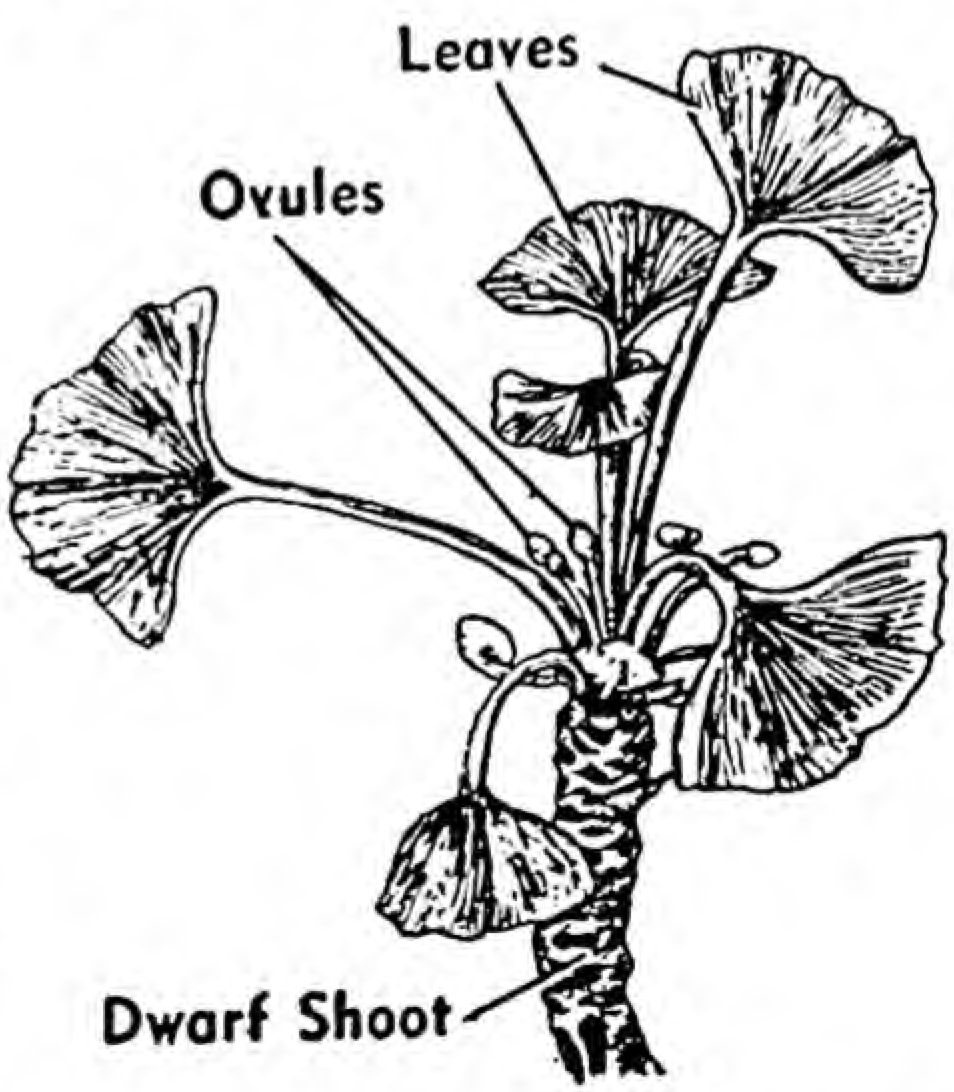



Fig. 5—9 A dwarf shoot of *Ginkgo biloba* with female reproductive organs and a cluster of leaves (After Foster & Gifford).

GAMETOPHYTIC GENERATION—The microspores or pollen grains (=the male gametophytes) germinate while still

enclosed in the microsporangium. The spore divides, a small prothallial cell is cut off (fig. 5-8A) and the larger cell divides again to form a second prothallial cell and an embryonal (antheridial) cell (fig. 5-8B). The first prothallial cell disintegrates soon while the second one persists. The embryonal (antheridial) cell divides to form a tube cell and a generative cell (fig. 5-8D). The microspores are shed at this four-celled stage (i.e., when they possess 2 prothallial cells—one developed and the other degenerated, a generative cell and a tube cell). Each microspore has two walls, the outer exine and the inner intine but the exine does not cover the spore entirely (fig. 5-8).

The microspores are carried by wind and ultimately reach the pollen chamber where they germinate further. The intine protrudes out to form a pollen tube (fig. 5-10). The generative cell divides to form a sterile cell and a spermatogenous cell. Blepharoplasts, as in *Cycas*, become prominent. Spermatogenous cell then divides to form two motile sperms possessing spiral bands of flagella as in *Cycas* (fig. 5-10C).

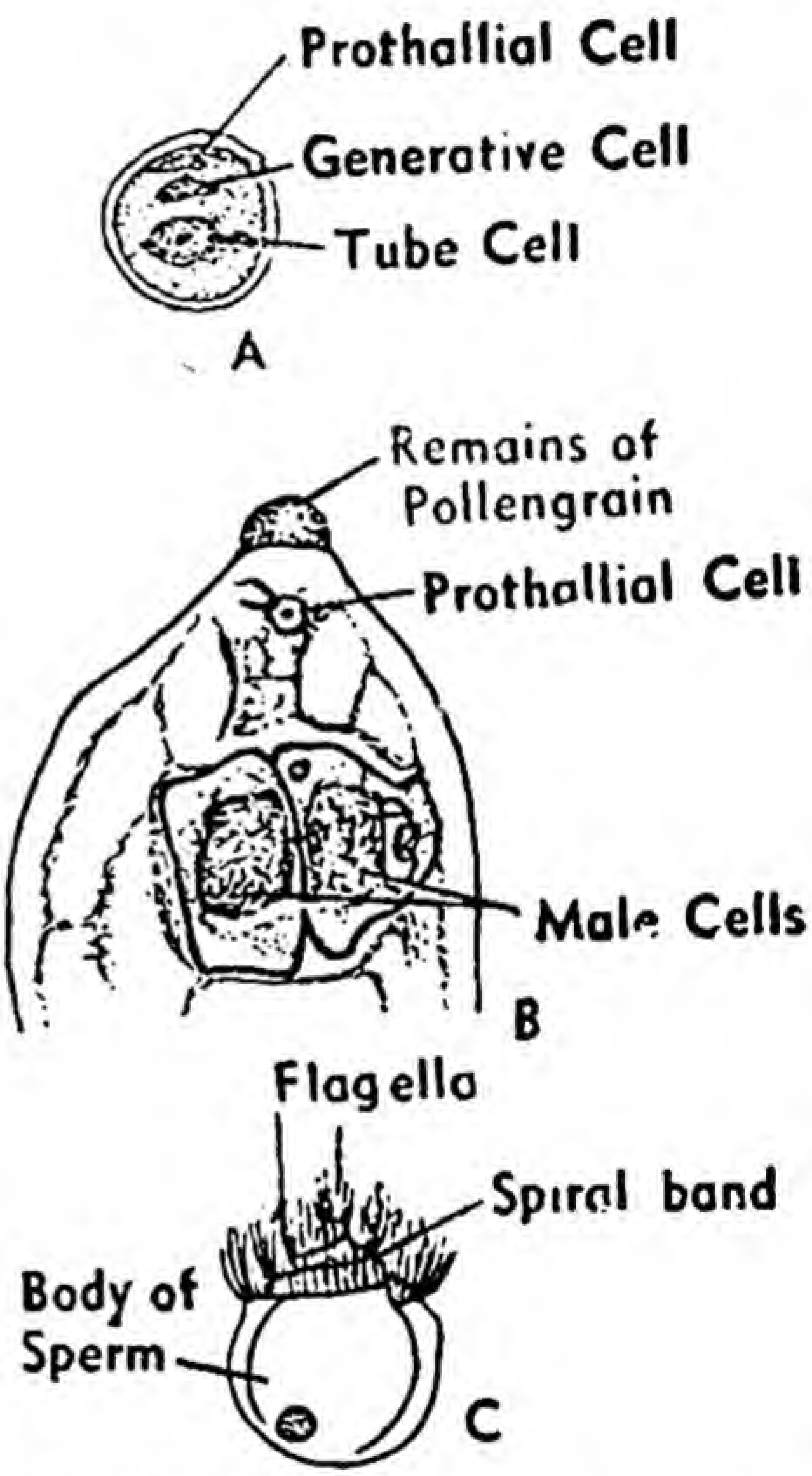



Fig. 5—10 Development and the structure of male gametophyte of *Ginkgo biloba*. A&B—Stages of the development of male gametophyte (After Hirase) C-a sperm (After Shimamura).

The functional megaspore representing the first cell of female gametophyte is elongate in form in the beginning, but becomes spherical later. Prior to pollination it undergoes free nuclear divisions as in *Cycas*. Wall formation starts after 13 free nuclear divisions have taken place. The number of free nuclei may be up to 8,000. Laying down of walls begins from the periphery and it proceeds towards

the centre, i. e., the growth is centripetal. After this the accumulation of starch, lipids and lipoproteins in the gametophytic tissue, starts.

Archegonial initials become recognisable as early as the end of June in France[1]. Usually two or rarely three archegonia develop towards the micropyle in each female gametophyte (fig. 5-11B). Each archegonium possesses a short neck made up of only four cells and a small venter possessing a central cell. The central cell later forms an egg cell and a ventral canal cell separated by a wall from the former (fig. 5-11A). In *Ginkgo* the archegonial chamber (fig. 5-11B) is like a crevice while in *Cycas* it is cup-

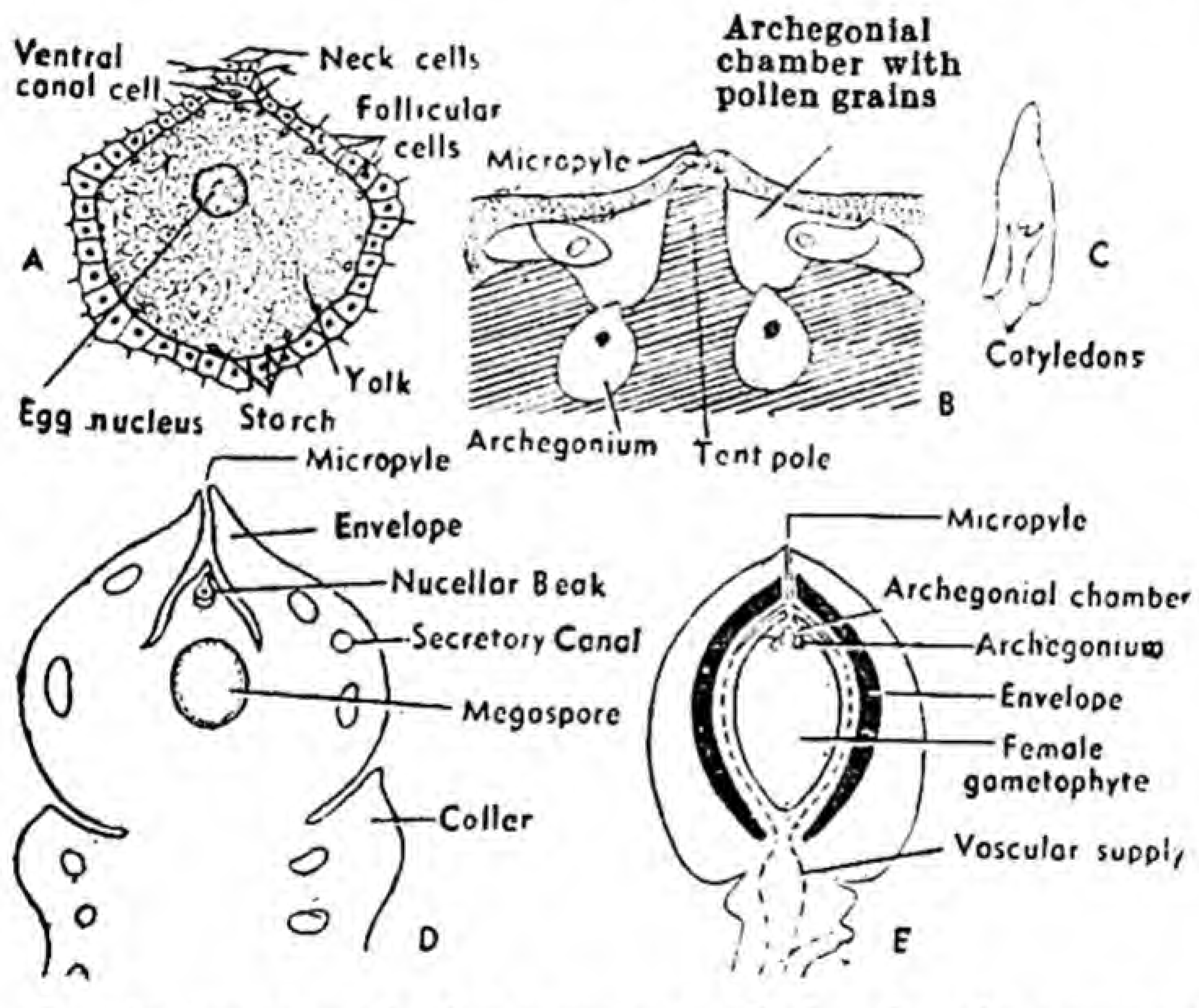



Fig. 5—11 Development and the structure of the female gametophyte and embryo in *Ginkgo biloba* A—L. S. of an archegonium (After Favre-Duchartre); B—L. S. at the apex of ovule showing a raised column like structure the 'tent pole' (shaded) and archegonial chamber (After Hirase); C—L. S. of the embryo (After Sprecher); D—L S. of the ovule showing nucellar beak, collar and envelope (After Coulter & Chamberlain); E—L. S. of the ovule, diagrammatic, modified from Sporne.

shaped. The female gametophyte is said to possess abundant chlorophyll[2]. Prior to fertilization the integument gets lignified. Pollinated ovules, if removed from mother plant, are capable of being fertilized.

1. Favre Duchartre, M. 1958.
2. Sporne, K.R. 1965 : 169.

**Fertilization**—The archegonial chamber gets moistened by the fluid discharged from the pollen tube. The egg and the sperm have 12 chromosomes each. Egg and sperm nuclei fuse together to form the zygote which now possesses 24 chromosomes.

DEVELOPMENT OF THE EMBRYO—After fertilization, which may occur either before or after the ovule has fallen from the tree, free nuclear divisions start again and result in the formation of nearly 256 free nuclei. Wall formation then takes place and the embryo becomes differentiated into three distinct regions. The middle and upper regions are conductive and haustorial in nature. Stem, root and cotyledons (fig. 5-11C) get differentiated from the basal portion of the embryo. Suspensor is not formed. Mucilage cavities occur in abundance in the young stem and cotyledons. A mature embryo possesses 2 to 5 cotyledonary leaves, two of which are decussate while the succeeding ones are arranged irregularly in the seedling.

**Structure of the seed**— The ovule even before fertilization may fall to the ground and the development of the embryo thus may take place there or it may take place on the tree. The seed (fig. 5-12) is protected by three distinct layers formed from the ovular envelope. The outermost is fleshy and emits unpleasant odour; the middle layer is hard and stony and the innermost turns watery in nature. The female gametophyte is edible and is eaten after roasting.

**AFFINITIES**—*Ginkgo biloba* is of great botanical interest because of the presence of a number of primitive as well as advanced characters.

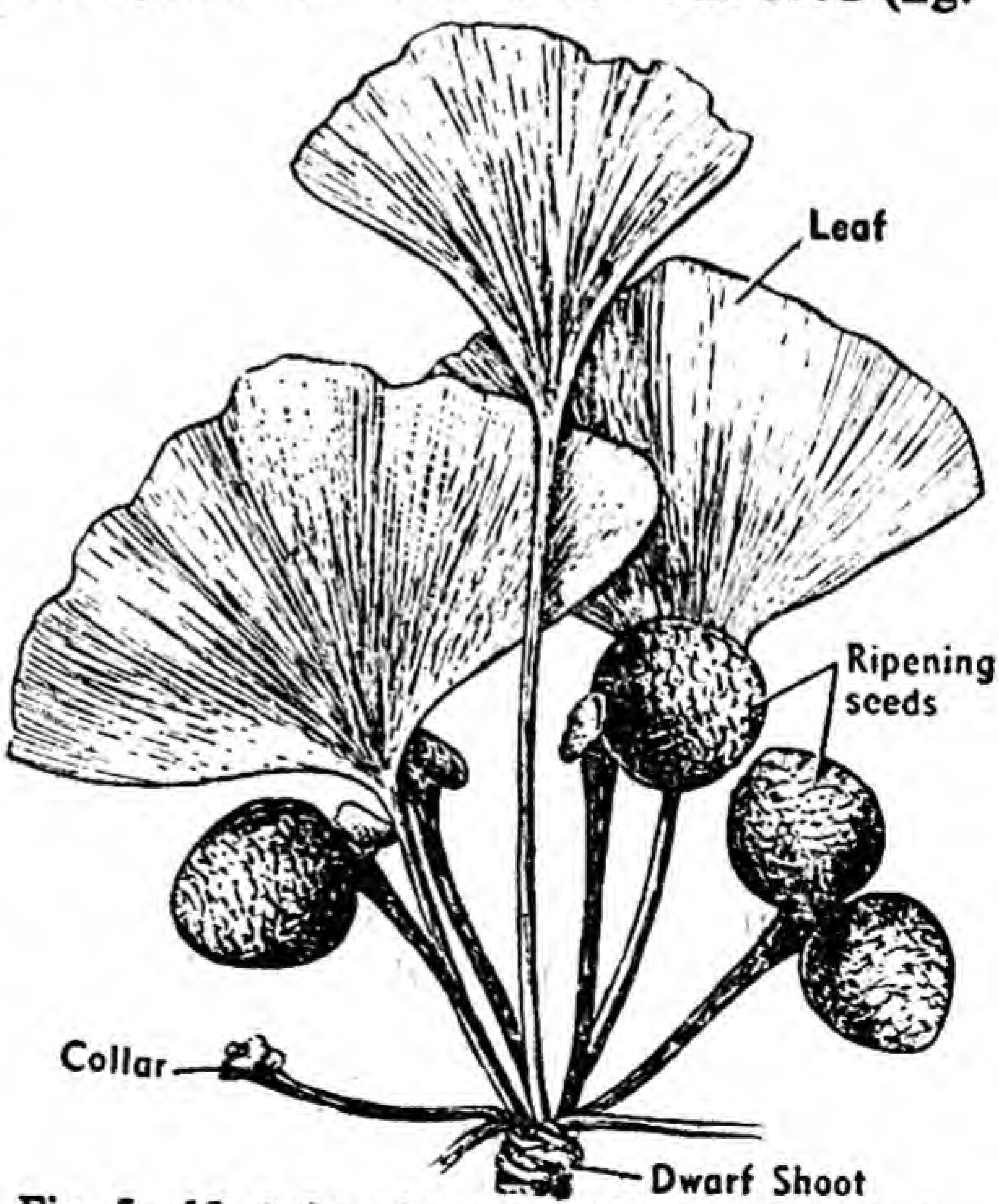


Fig. 5—12 A dwarf shoot of *Ginkgo biloba* with leaves and ripening seeds (After Foster & Gifford).

**Resemblances with the Cycads**—The presence of wide pith, cortex and a large number of mucilage ducts in stem, leaf, petiole, root and embryo, are characters common to both. The presence of mesarch xylem in the cotyledonary and adult leaves, eusporangiate development of microsporangia, foliar nature of micro- and megasporophylls, presence of a nucellar beak, pollen chamber, multiflagellate sperms and free-nuclear divisions during the development of the embryo are some of the characters in which *Ginkgo* resembles the cycads. Both *Cycas & Ginkgo* are primitive gymnosperms. The presence of a crown of leaves and leaf-scars on the dwarf shoots are features which may also be regarded as primitive. They have remained at the prephanerogamic stage.

**Resemblances with Pteridosperms and Cordaitales**—The accumulation of abundant reserve food material, the lignification of the ovular integument prior to fertilization are considered primitive characters. These characters are shared by Pteridosperms and Cordaitales. In addition fertilization and subsequent development of embryo in the ovules, detached from mother plant, can be induced in *Ginkgo*. That probably also occurred in the Pteridosperms and Cordaitales. Because of these primitive characters the Pteridosperms, Cordaitales and Ginkgoales are sometimes called Prephanerogams.[1]

**Resemblances with the Conifers**—The presence of annual rings in the secondary wood of stem and root, compact or pycnoxylic nature of secondary wood, narrow rays, tree-like habit of the plant, the presence of dimorphic shoots and leaves with sunken stomata are the characters in which it resembles the conifers.

The bilobed form of leaves, biseriate pitting in the tracheids, presence of trabeculae, crevice-like archegonial chamber, absence of a suspensor from the embryo, presence of a collar round the ovule, 'tent pole' and unequal size of cotyledons are important characters which are present neither in the cycads nor in the conifers. These characters justify an independent and distinct status for the Ginkgoales.

1. Favre Duchartre M. 1958.

Chapter 6

# Cordaitales

Cordaitales are believed to have formed the dominant arborescent vegetation of the Carboniferous and the Permian periods. Representatives of this order have been found in Europe, North and South America, China, Russia, India, Australia and Africa. Such a distribution denotes their worldwide occurrence at that time. Cordaitalean remains generally occur in the form of compressions.

DISTINGUISHING FEATURES—The order includes large trees with monopodial habit, possessing a whorl of branches. Some of these are presumed to have attained a height of nearly 30 metres. Primary wood was poorly developed, while the secondary wood, like that of the conifers, was abundant and pycnoxylic. Leaves were spirally arranged; they assumed different shapes and dimensions in different sub-genera. Trees were dioecious and the strobili were unisexual. Each strobilus consisted of a main axis bearing sterile and fertile bracts. The fertile bracts or sporophylls subtended microsporangiate and megasporangiate organs. Each microsporophyll bore 4 to 6 microsporangia and each megasporophyll possessed 1 to 4 ovules or megasporangia. The seeds were bilaterally symmetrical.

CLASSIFICATION—The order has been divided into three families, viz., Eristophytaceae, Cordaitaceae and Poroxylaceae; of these, the Cordaitaceae is the best known.

The following form genera are described:

Stem ... *Cordaites* Unger., *Mesoxylon* Scott and Maslen.
Leaves ... *Cordaites* Unger.
Root ... *Amyelon radicans* Williamson
Strobili ... *Cordaitanthus* Otto Feistm. (=*Cordaianthus* Grand 'Eury)
Seeds ... *Cardiocarpus* Brongn. (=*Cordaicarpus H. B.* Geinitz.)

MORPHOLOGICAL FEATURES—*Cordaites* Unger. (the form-genus for stem and leaves) possessed a long and slender stem which bore spirally arranged leaves (fig. 6-1). On the basis of the form and dimensions of leaves *Cordaites* is further subdivided into 3 sub-genera viz., *Eucordaites, Dorycordaites* Zeil. and *Poacordaites* Grand 'Eury. *Eucordaites* possessed broad leaves with a blunt apex while *Dorycordaites* possessed leaves with pointed apex. The broad leaves in these two subgenera measured nearly 100 cm in length and 15 cm in width; they were simple, strap-shaped or spatulate in form and tough and leathery in texture (fig.6-1). Venation was actually dichotomous, but the branches of veins ascended so steeply that they

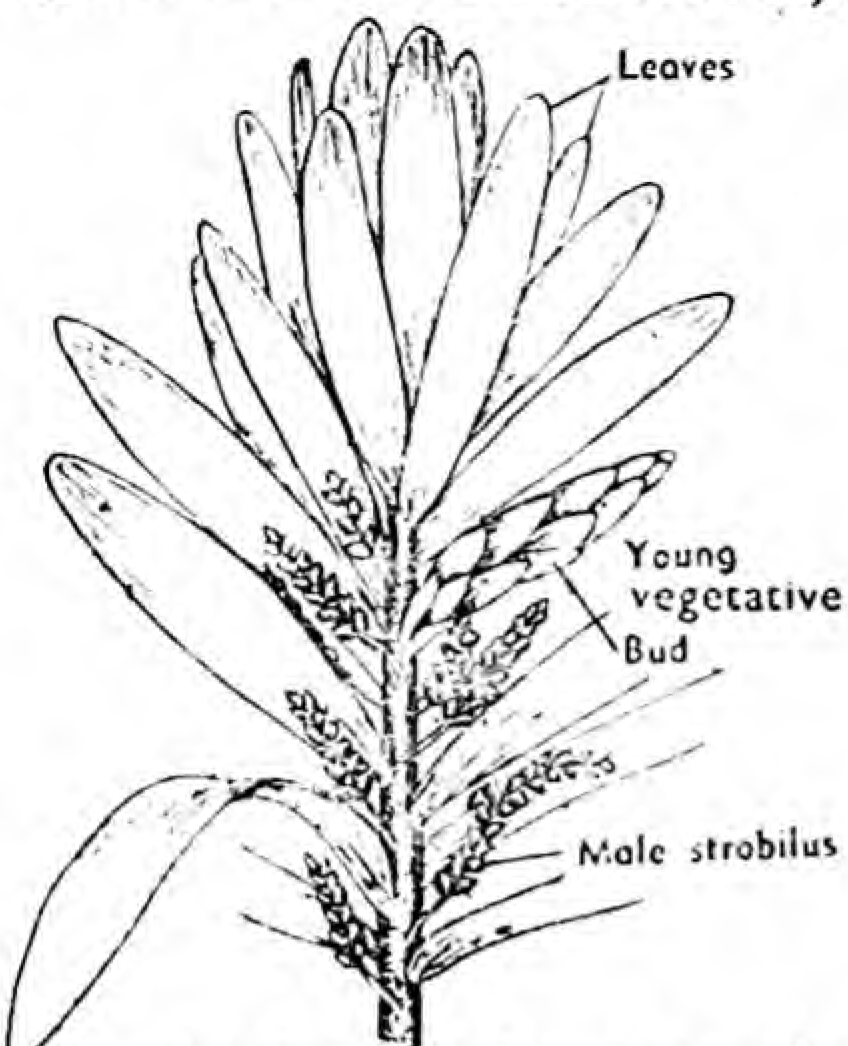



Fig. 6—1 Portion of the stem of *Cordaites* with leaves and male inflorescences (After Grand 'Eury).

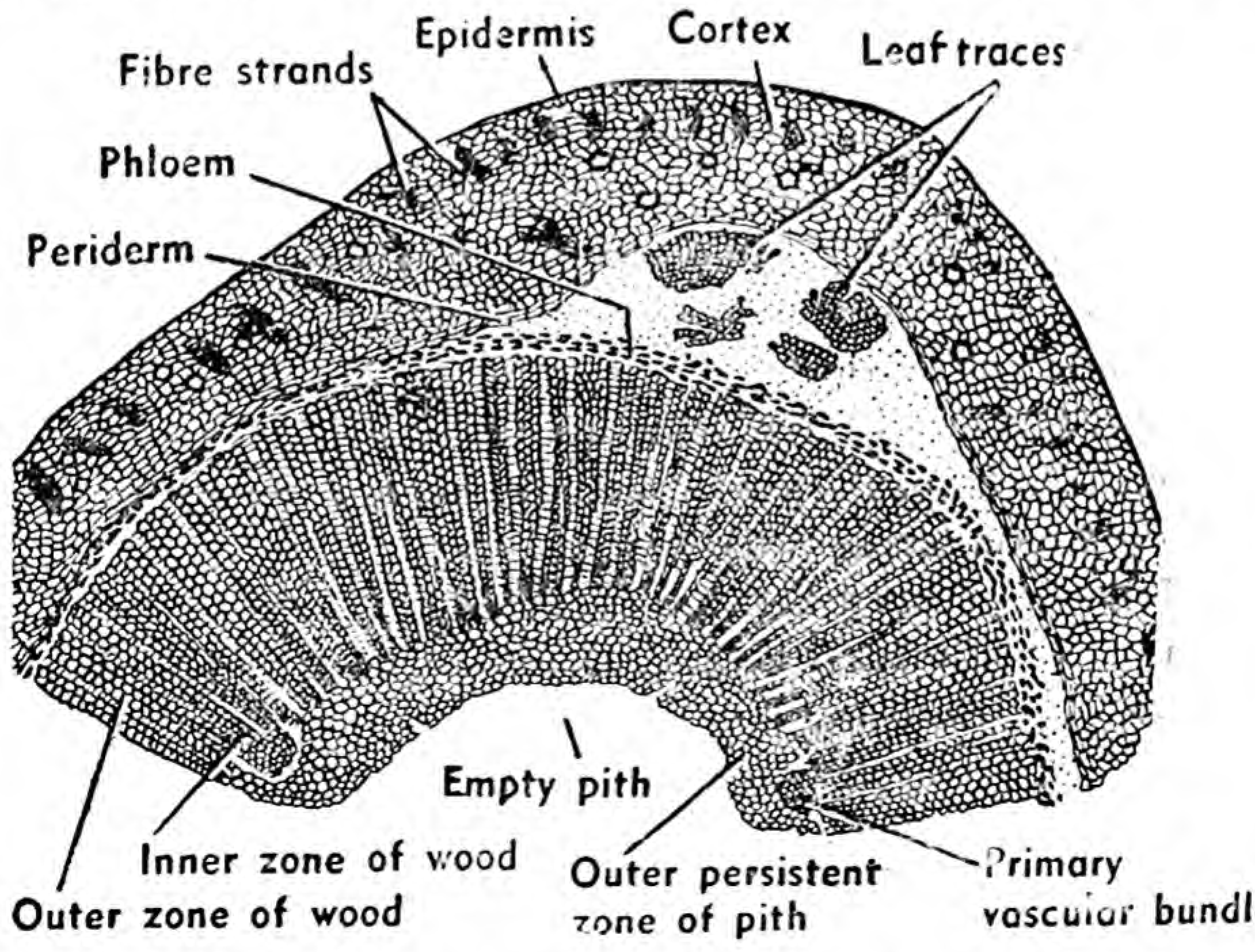



Fig. 6—2 T. S. of stem of *Cordaites* (After Renault).

appeared almost parallel. The veins possessed I-shaped girders of thickened cells between them. The leaves in *Poacordaites* Grand 'Eury were quite small, about 3 cm in width and grass-like in form.

HISTOLOGICAL FEATURES—*Cordaites* and *Mesoxylon* both possessed a centrally-situated large pith which was characteristically discoid (fig. 6-4&5). This appearance was due to transverse ruptures which occurred in the pith in many places, leaving numerous diaphragms separated by empty spaces. Pith was continuous in *Metacordaites* Renault and also in *Dadoxylon zalesskyi* Sahni. The amount of primary xylem was small as compared to the secondary which was well developed (fig. 6-2). Primary xylem consisting of smaller and narrower tracheids was situated in the form of patches at the apices of the wedges of secondary wood (fig. 6 2). In between the wedges towards the pith in *Cordaites michiganensis* occur broad xylem rays (fig. 6-3). Primary and secondary woods were not sharply demarcated. Except in *Mesoxylon* and *Parapitys zalesskyi*, where the xylem was mesarch, the primar


Fig. 6—3 T.S. of the inner part of the wood of *Cordaites michiganensis* showing narrowing secondary wood wedges towards the pith. Primary wood is not distinct (After Arnold).

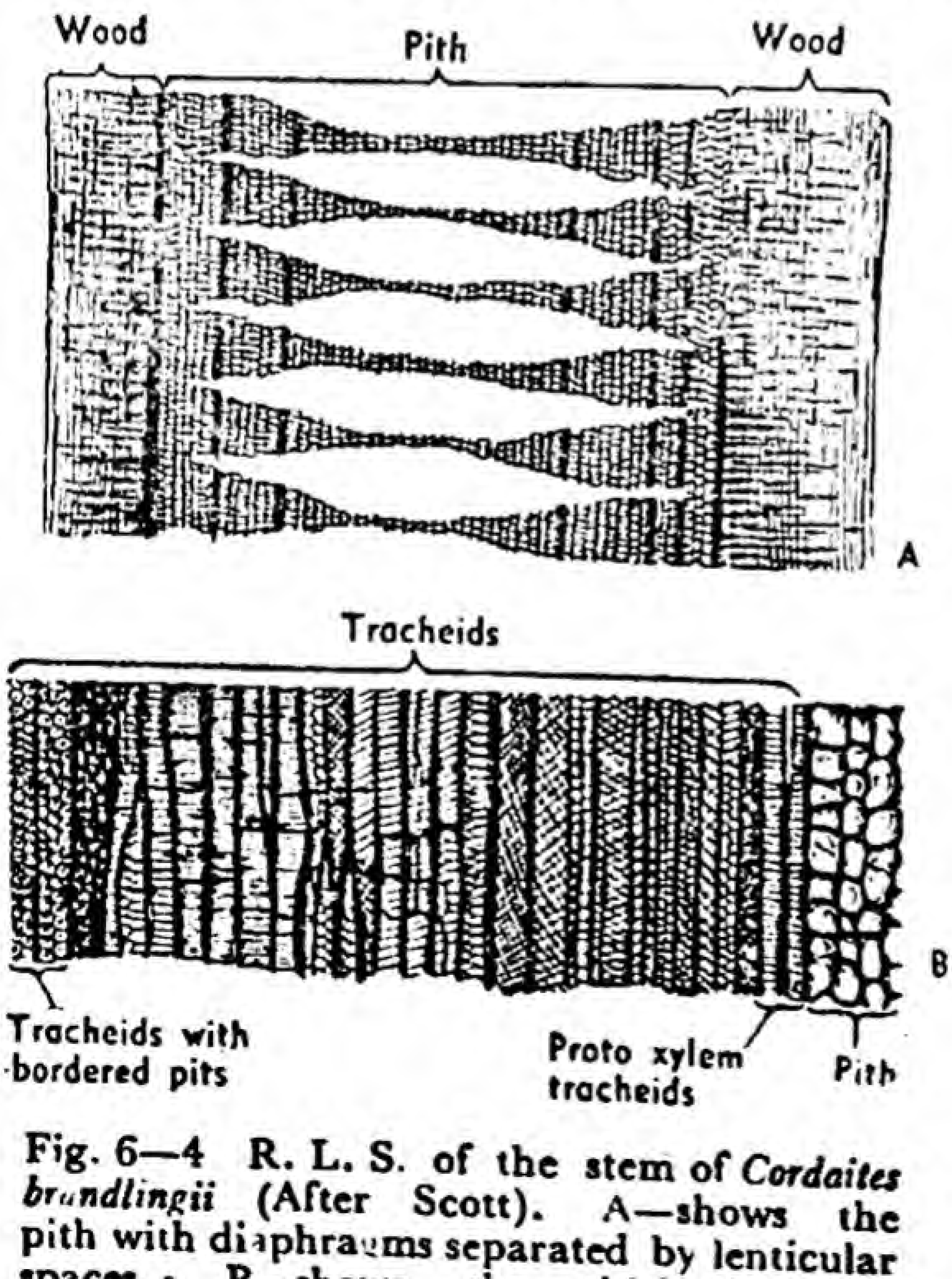



Fig. 6—4 R. L. S. of the stem of *Cordaites brandlingii* (After Scott). A—shows the pith with diaphragms separated by lenticular spaces ; B—shows the thickenings of tracheids.

xylem was endarch. Traverse[1] reports mesarch condition in *Cordaites* though the amount of centripetal xylem is meagre.

The secondary wood consisted of long and slender tracheids possessing biseriate, triseriate or multiseriate bordered pits on their radial walls (fig. 6-4). Rays were simple and narrow, usually one cell wide. Some of the cells of the ray possessed resinous contents. Xylem parenchyma and resin canals, as in the conifers, have not been found.

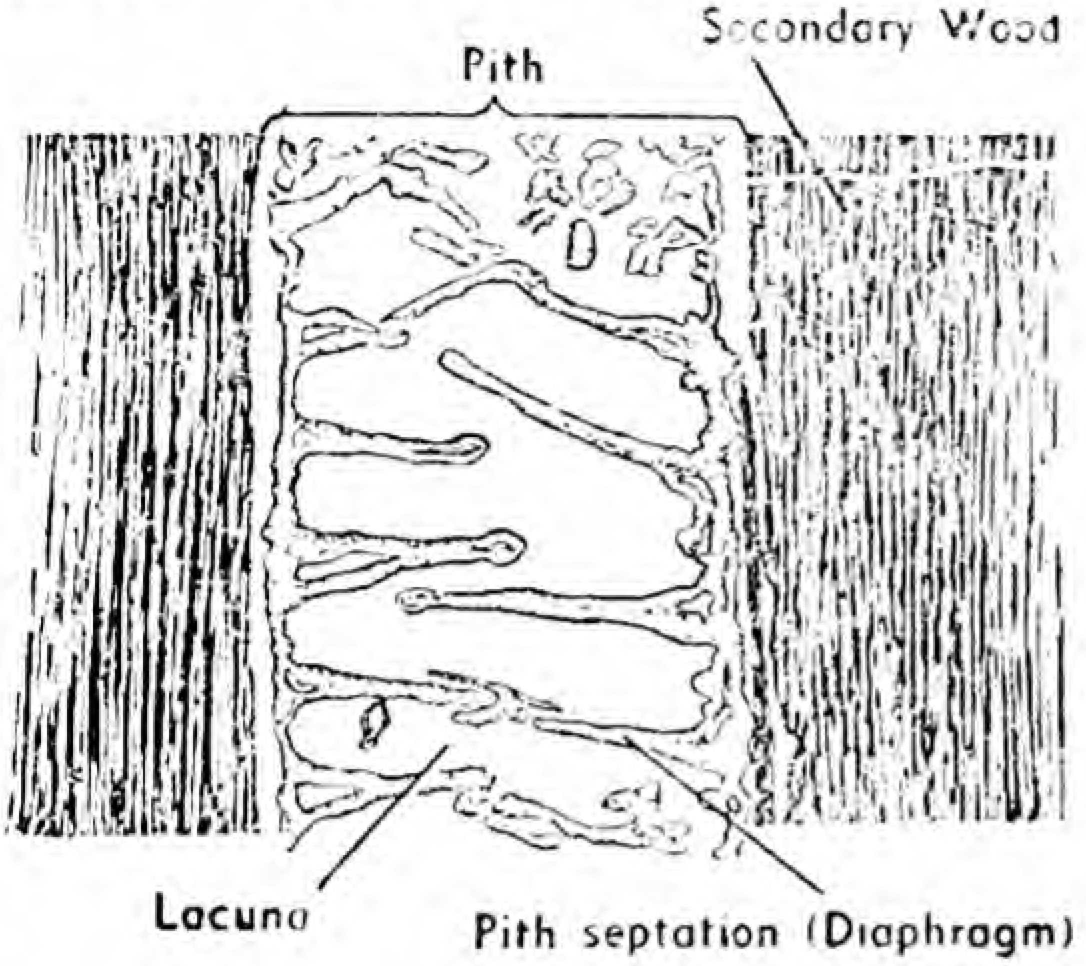



Fig. 6—5 R. L. S. of the stem of *Cordaites traversa* showing lacuna and diaphragms in the pith (After Arnold).

The leaf-trace bundles of *Cordaites* resembled those of the cycads in their pseudomesarch or diploxylic nature. Each leaf was supplied by a pair of traces as in the Ginkgoales. These traces, however, unlike those of *Ginkgo*, arise from a single protoxylem group.

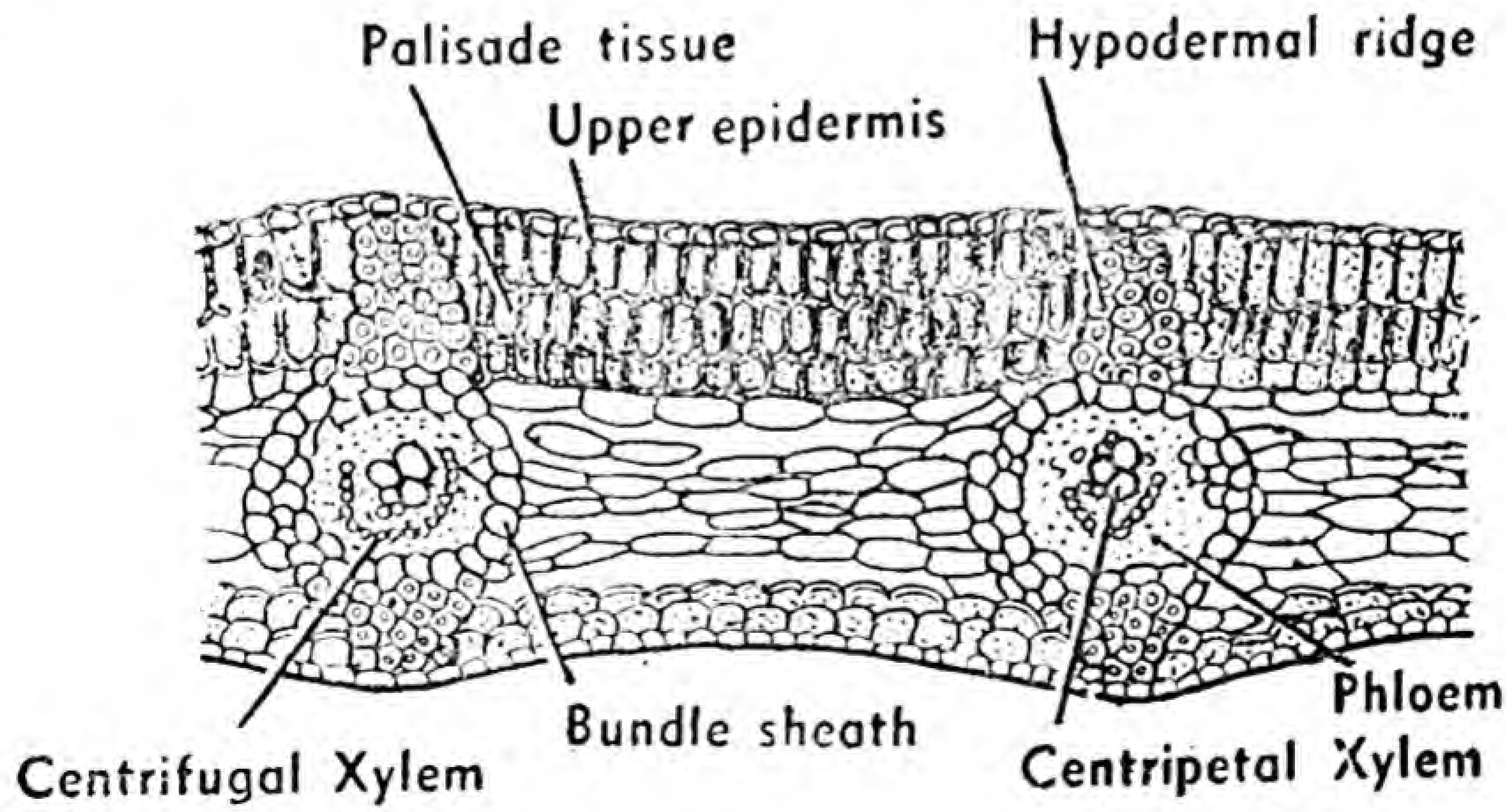



Fig. 6—6 T. S. of the leaf of *Cordaites lingulatus* (After Renault).

The leaves of *Cordaites* presented considerable variations in their internal structure; they possessed thick cuticle and longi-

1. Traverse, A. 1950.

tudinally disposed stomata (fig. 6-7). In some species stomatiferous bands were separated from one another by non-stomatiferous strips. Guard cells were surrounded by 4 to 6 subsidiary cells. Cuticular ridges and papillae have also been observed. Each stoma possessed 2 polar & 2 to 4 lateral subsidiary cells (fig. 6-7). In *C. lingulatus*, the palisade and spongy tissues were well differentiated (fig. 6-6) but in *C. angulosostraitus*, these were not differentiated and hence the photosynthetic tissue appeared uniform throughout.

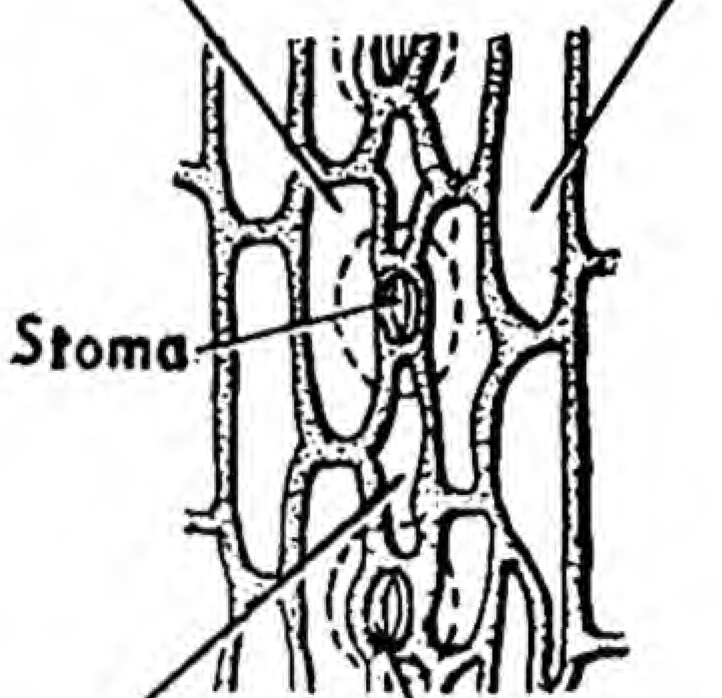



Fig. 6—7 Portion of the epidermis of *Cordaites* with details of stomatal structure (After Florin).

*Amyelon radicans*, regarded as the root of *Cordaites*, was diarch to tetrarch. It consisted of a central protostele which was surrounded on its outer side by secondary xylem. Periderm was formed well within the cortex (fig. 6-8).

Cordaitean trees were dioecious.

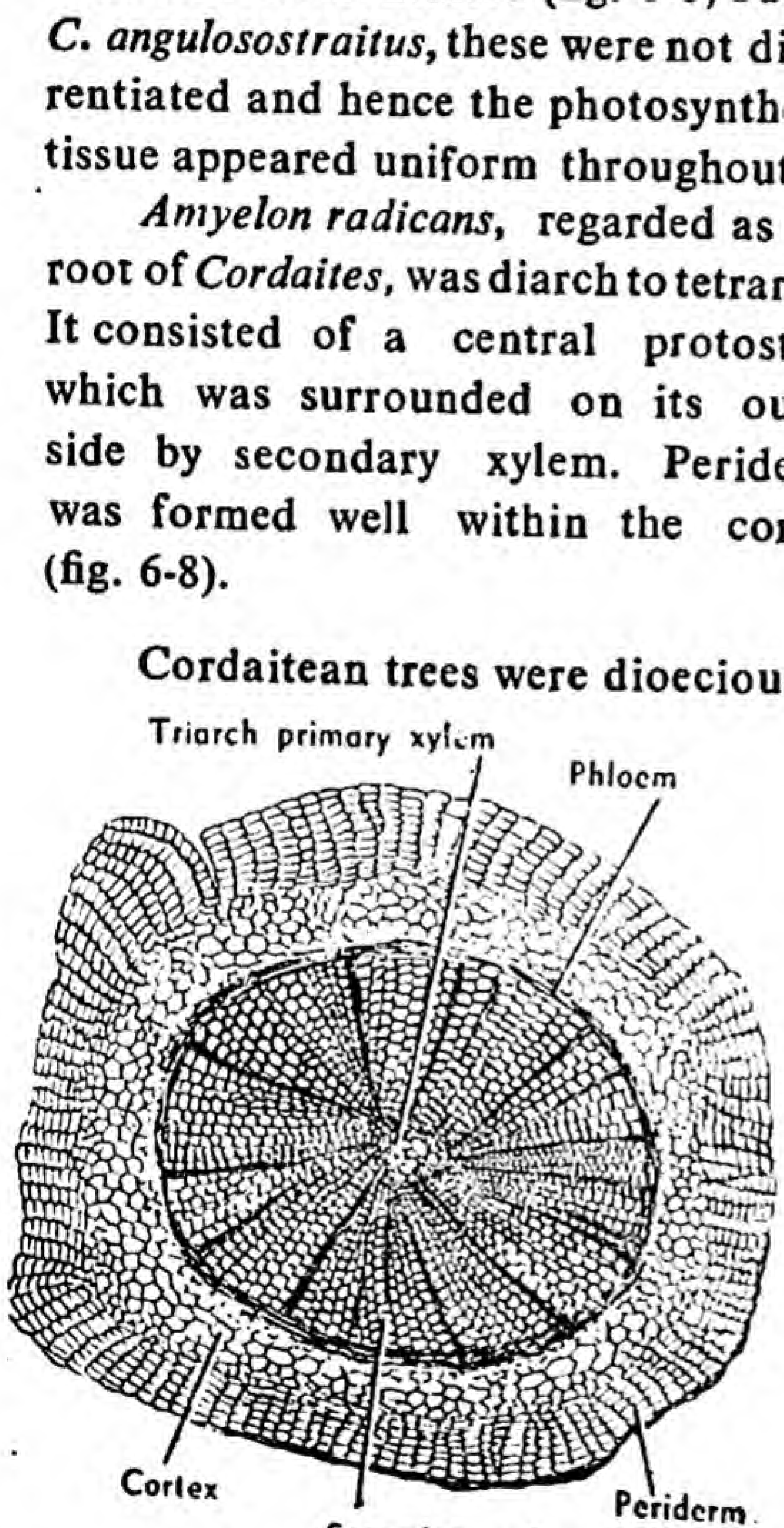



Fig. 6—8 T. S. of *Amyelon radicans*, the root of Cordaites (After Scott).

**LIFE-HISTORY**

The individual strobili or fructifications, called *Cordaitanthus* or *Cordaianthus* were unisexual, and measured nearly 1 cm in length.

The male strobili possessed a stout central axis which bore numerous sterile bracts and a few microsporophylls. Each microsporophyll possessed 1 to 6 microsporangia (fig. 6-9). According to Delevoryas[1], *Cordaitanthus concinnus* had a short axis, 1to2 mm in diameter. It bore two rows of dwarf shoots which were situated in the axils of the bracts. Each dwarf shoot, about 6 mm

1. Delevoryas, T. 1953.

long, possessed spirally arranged, 25 to 40 closely imbricated scales.

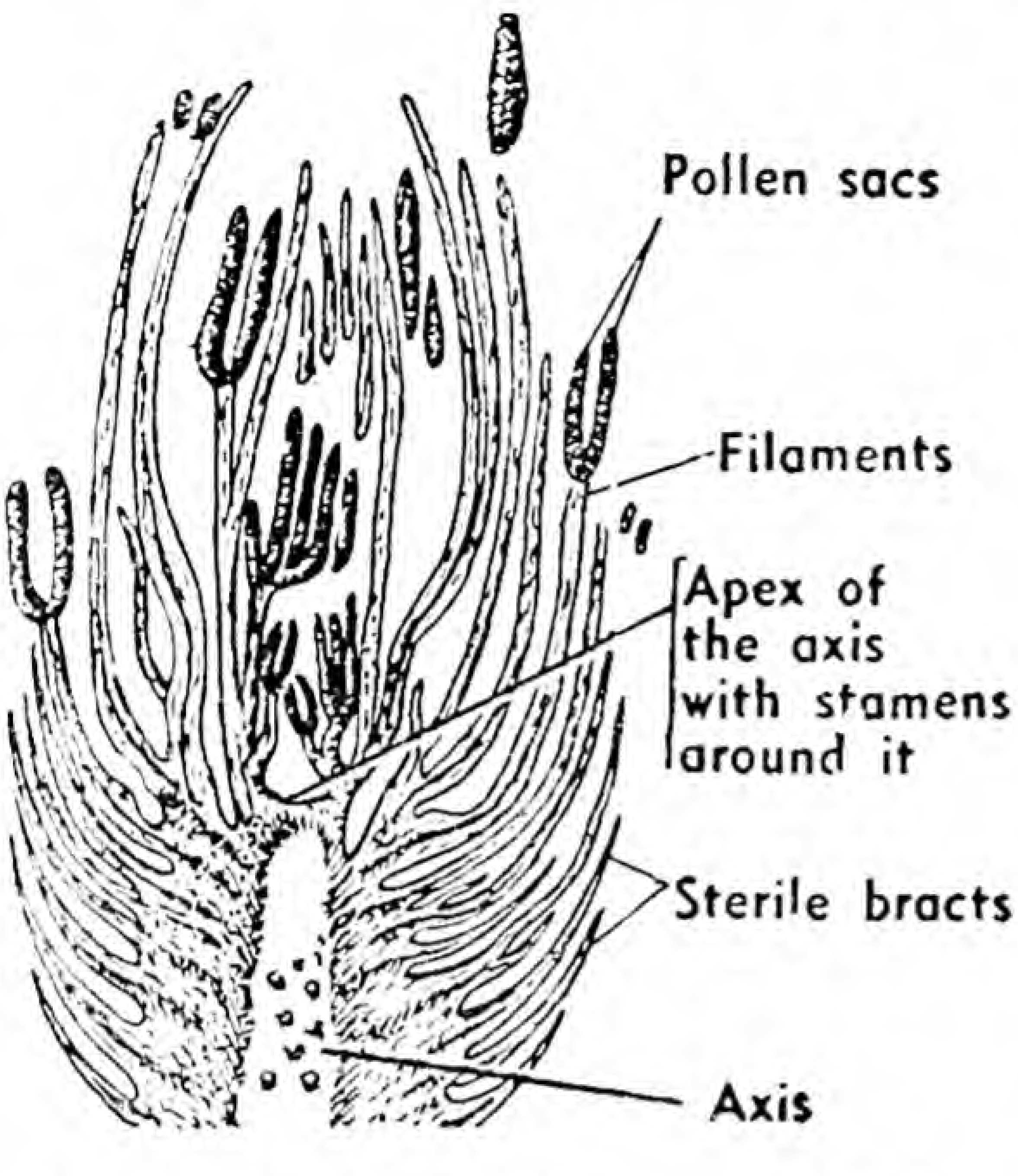



Fig. 6—9 L. S. of *Cordaitanthus penjonii*, the male reproductive organs of *Cordaites* (After Renault).

The fertile scales (=microsporophylls), situated distally, possessed 6 sporangia apically (fig. 6-10). Each microsporangium measured one mm. in length. The microsporangia were fused at the base. *Cordaitanthus penjonii*, described from France, also possessed 6 terminal microsporangia.

The female strobili, like the male ones, also had a stout axis which had a large number of spirally arranged bracts. In some species these strobili measured about 30 cm in length. The bracts subtended in their axils short secondary fertile shoots, bearing spirally arranged sterile and fertile bracteoles (or megasporophylls). *Cordaitanthus pseudofluitans* possessed a few distally borne, elongated and dichotomously branched fertile megasporophylls. Each megasporophyll at its apex possessed 2 or more ovules. The number of fertile bracteoles in a strobilus was about 4, sometimes only one was present as in *Cordaitanthus zeilleri* and *C. williamsonii* (fig. 6-11). The nucellus of the ovule remained free from the envelope for

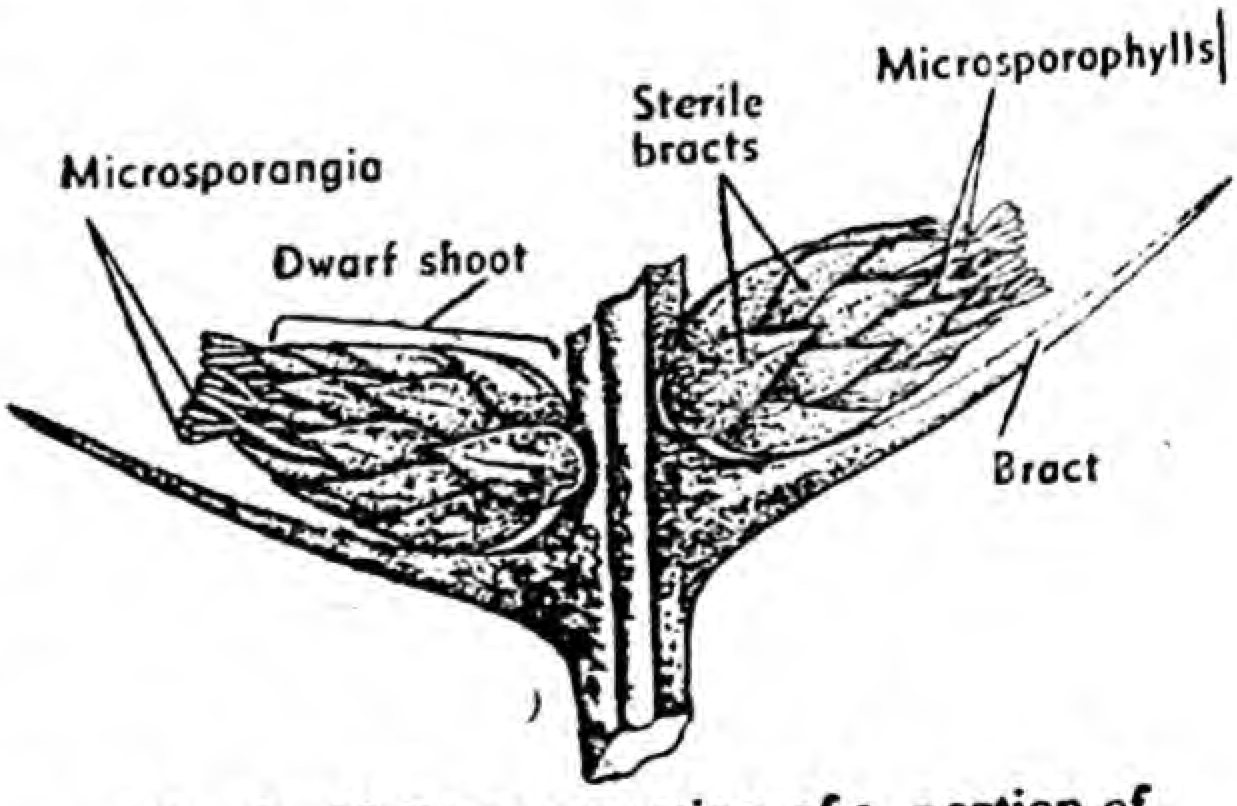



Fig. 6—10 Reconstruction of a portion of *Cordaitanthus concinnus* with two male strobili (After Delevoryas).

most of its length. A pollen chamber was present (fig. 6-12).

GAMETOPHYTIC GENERATION—Not much is known of the gametophytes except that the male gametophytes or pollen grains (microspores) of Cordaitales were globoid in shape and measured nearly 100μ in diameter. Each had a thick cutinized wall, exine and a thin inner, intine. The exine formed a large air sac as a result of its being free from the intine for a large part (fig. 6-13). Pollination was probably anemophilous. Nuclear divisions occurred during the germination of male gametophyte.

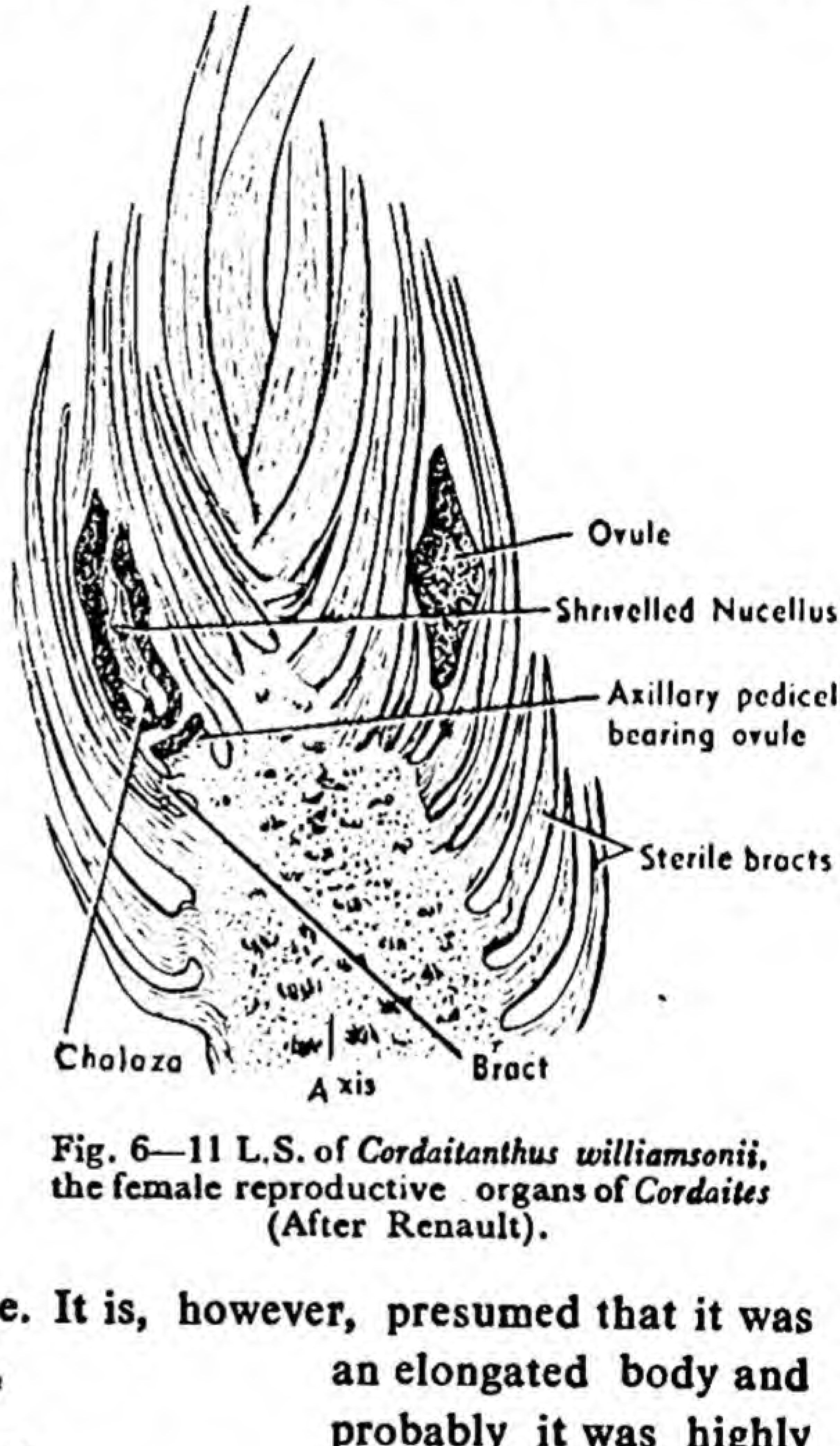



Fig. 6—11 L.S. of *Cordaitanthus williamsonii*, the female reproductive organs of *Cordaites* (After Renault).

Nothing definite is known about the details of the female gametophyte. It is, however, presumed that it was an elongated body and probably it was highly developed. The megaspore membrane was simple in structure resembling the exine of pteridophytic spores[1].

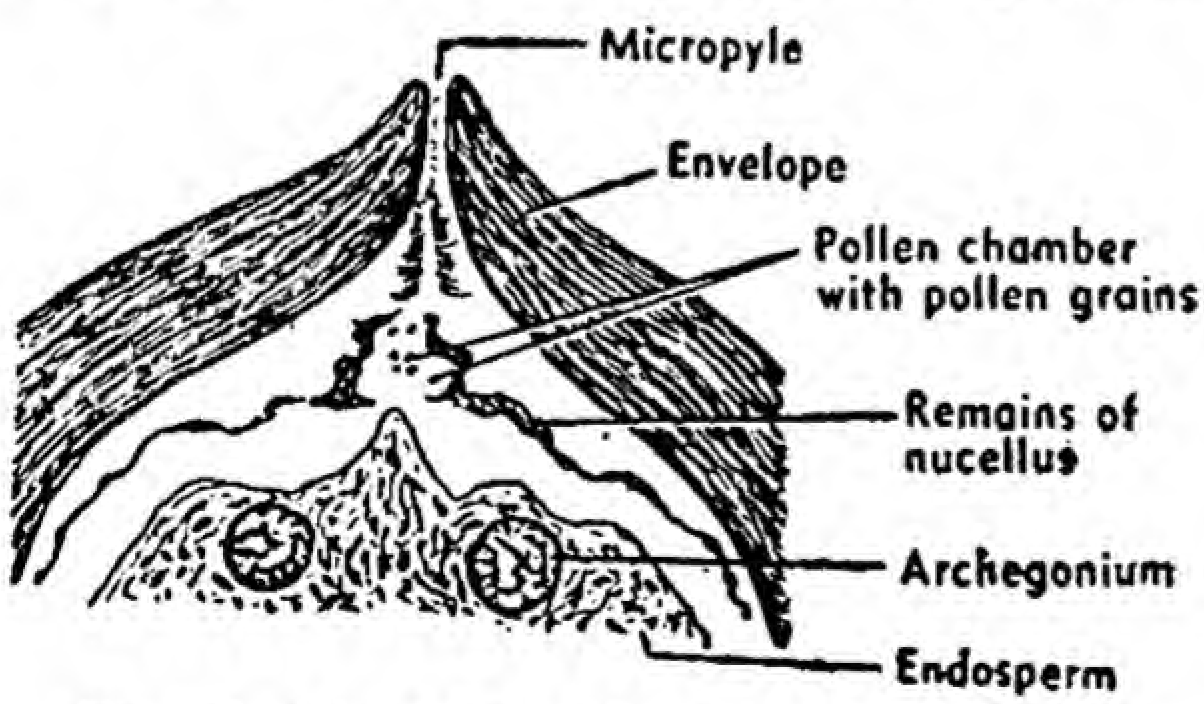



Fig. 6—12 L.S. of the apical portion of *Cycadinocarpus angustodunensis* (After Renault).

STRUCTURE OF SEED—It is presumed that *Cordaitanthus* (=*Cordaianthus*) type

1. Pettit, J. M. 1966.

of strobili possessed seeds, known as *Cardiocarpus* (=*Cordaicarpus*) (fig. 6-14). *Cardiocarpus* (the generic name given to flattened, heart-shaped seeds) were bilaterally symmetrical. They possessed nucellus in the centre which was surrounded by a two-layered envelope. Probably the outer layer of envelope expanded into an encircling wing. The basal portion of the seed was round or cordate in shape, while the apical portion was drawn out in the form of a beak (fig. 6-12). The nucellar beak projected upwards into the micropyle. *Cardiocarpus* (=*Cordaicarpus*) *spinatus* was a fairly large seed, almost equally long and broad. It consisted of five distinct layers, viz, outer and inner sarcotesta; outer and inner sclerotesta, and endotesta (fig. 6-15). A few other seeds with doubtful cordaitalean affinities are :

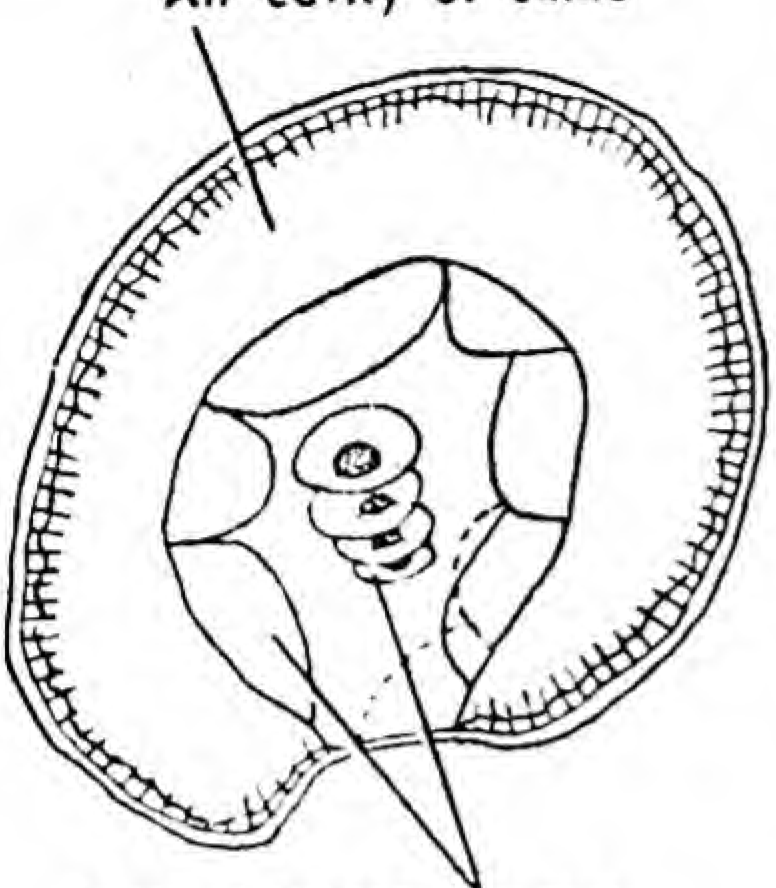



Fig. 6—13 A pollen grain of *Cordaitanthus sp.* with internal details (After Florin).

*Kamaraspermum leeanum* Kern, *Codonospermum olivaeforme* Renault, *Cardiocarpon*, *Cycadinocarpon*, *Diphotesta*, *Mitrospermum*, etc.

Cordaitalean remains known from India[1] are :

**Leaf-genera**— *Noeggerathiopsis hislopi* (Bunb.) Feistm., *N. stoliczkanus* (Feistm.) Arber, *Euryphyllum whittianum* Feistm.

**Stem-genera** — *Dadoxylon bengalensis* Holden, *D. indicum* Holden, *D. zalesskyi* Sahni.

**Seed-genera**—*Cordaicarpus furcatus* Surange and Lele, *Samaropsis indica* (Zeillar) Seward, *S. milleri* (Feistm.) Seward and *S. raniganjensis* Seward and Sahni.


Fig. 6—14 Portion of *Cordaitanthus sp.* bearing seeds (After Berry).

1. Sitholey, R. V. 1963.

## AFFINITIES

Cordaitales appear to be a well-developed order of plants that existed far back in the Palaeozoic. They show certain characters which find parallel in some living cycads and conifers.

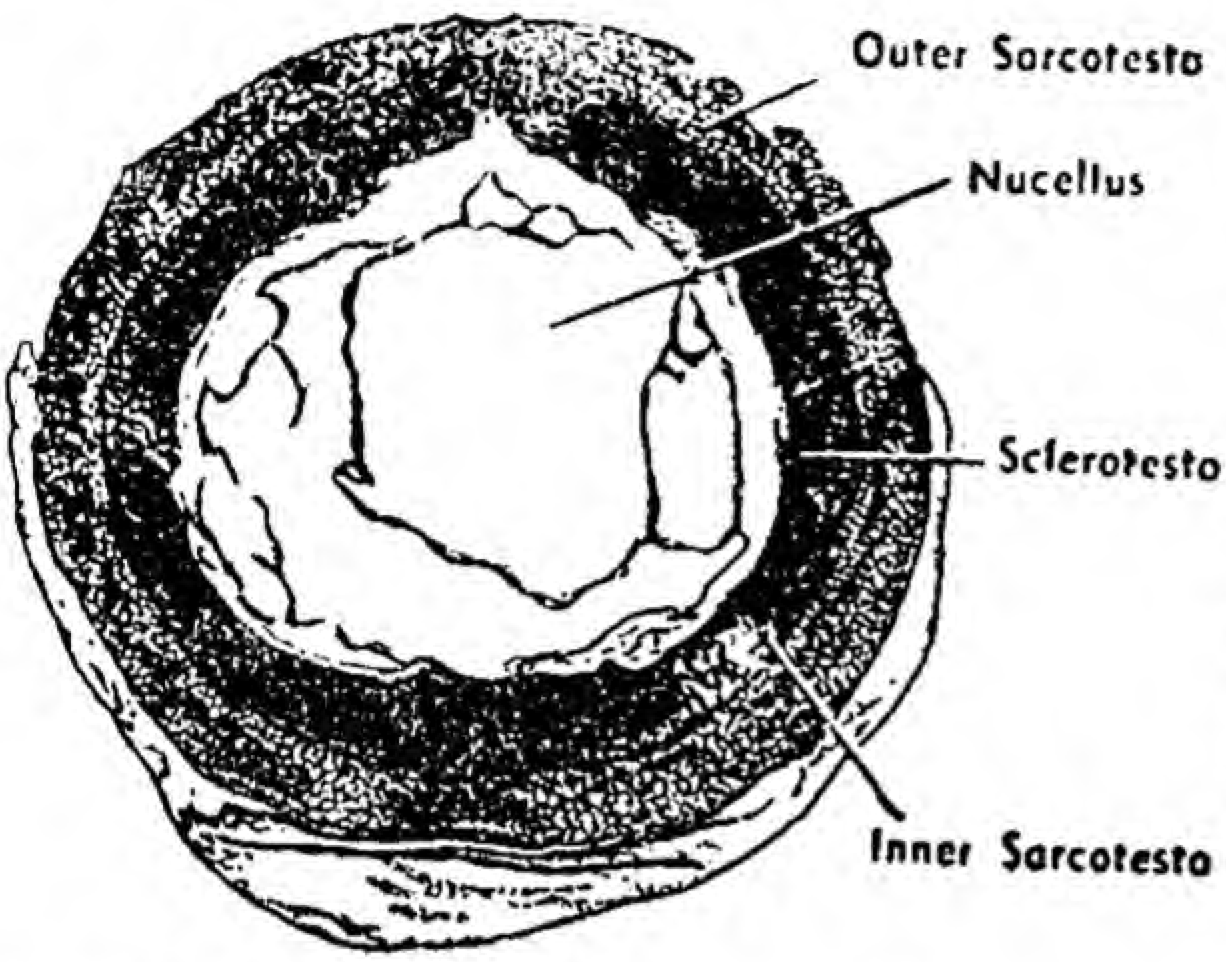



Fig. 6—15 L. S. of *Cardiocarpus spinatus*, the seed of *Cordaites* with 5-layered envelope. Broken lines indicate endotesta (After Baxter).

**Resemblances with the Cycads**—The presence of large pith and cortex, the internal structure and mesarch vascular bundles of the leaves, the general structure of ovule and seed suggest affinities with the cycads.

**Resemblances with the Conifers**—The arborescent habit is common to both the Cordaitales and the conifers while the parallel veined leaves of *Cordaites* resemble those of *Podocarpus* and *Agathis*. The secondary wood in both is well developed, i. e., pycnoxylic. In the presence of multiseriate, angular bordered pits and in the absence of resin canals the Cordaitales approach *Araucaria*. Further, the strobili of palaeozoic Conifers like *Lebachia* Florin, *Pseudovoltzia* Florin, etc., are very similar to the cordaitalean strobili in their morphology.

In having parallel veined leaves and double leaf-trace the Cordaitales show resemblances with the Ginkgoales.

# Chapter 7

# Coniferales

GENERAL CHARACTERS—This order now comprises six families, namely, Pinaceae, Taxodiaceae, Cupressaceae, Araucariaceae, Podocarpaceae and Cephalotaxaceae. True conifers like *Pinus*, *Thuja*, *Araucaria* etc., are cone-bearing plants. But in *Cephalotaxus* and *Podocarpus* the cone formation in the female inflorescence is not apparent. Coniferales constitute the largest order of the living Gymnosperms[1]. The plants may be monoecious or dioecious, i. e., male and female strobili may be borne on the same or different plants, respectively. It is the most dominant and widely distributed order of the gymnosperms and is represented by 54 genera and 482 species.[2] Amongst these, about 30 genera are confined to the northern and the rest to the southern hemisphere. The plants thrive well in temperate climate. Plants of this order range from shrubs to gigantic trees. Some of the tallest trees of the world, *Sequoia* and *Sequoiadendron* belong to this order. Some of these may be very old attaining an age of about 4,000 years. The fossil representatives of the order have been collected from the late Carboniferous and the early Permian deposits.

DISTINGUISHING FEATURES—The plants belonging to this order have the distinguishing features given below:

They are mostly xerophytic, evergreen trees or rarely shrubs with monopodial growth, the stem forms the main shaft; lateral branches are many. Leaves are simple, narrow, needle-like or scaly, rarely broad, spirally arranged or opposite, rarely whorled, evergreen, sometimes falling in autumn as in *Larix* and *Taxodium*. Phyllotaxy is spiral, distichous or

1. Coulter, J. M. and C. J. Chamberlain 1910.
2. Hui-Lin Li 1952.

whorled. Leaves are solitary or in fascicles. They possess resin canals. Wood is dense, massive, or pycnoxylic and without vessels. It is made up of long tracheids possessing large uniseriate rarely multiseriate bordered pits on their radial walls and small wood rays. Wood generally possesses resin canals. Strobili (=cones) are terminal or axillary, formed of compactly arranged sporophylls. Most of the genera are monoecious e. g., *Pinus*, whereas a few are dioecious, e. g., *Juniperus*. Female strobili consist of an axis with many to a few bract scales, each subtending or fused with an ovuliferous scale. Male strobili are simple. Microsporophylls (=stamens) are stalked, small, many in number; they are scale-like and bear 2 to 15 or rarely more microsporangia on their lower surface (fig 7-1). Connective may often be prolonged as an appendage. Microspores (=pollen grains) are numerous, winged as in *Pinus* or unwinged as in *Taxodium*. Megasporangia (=ovules) are eusporangiate and are diverse in appearance. Their number varies from 2 to many rarely only one ovule may be present on each megasporophyll. Female

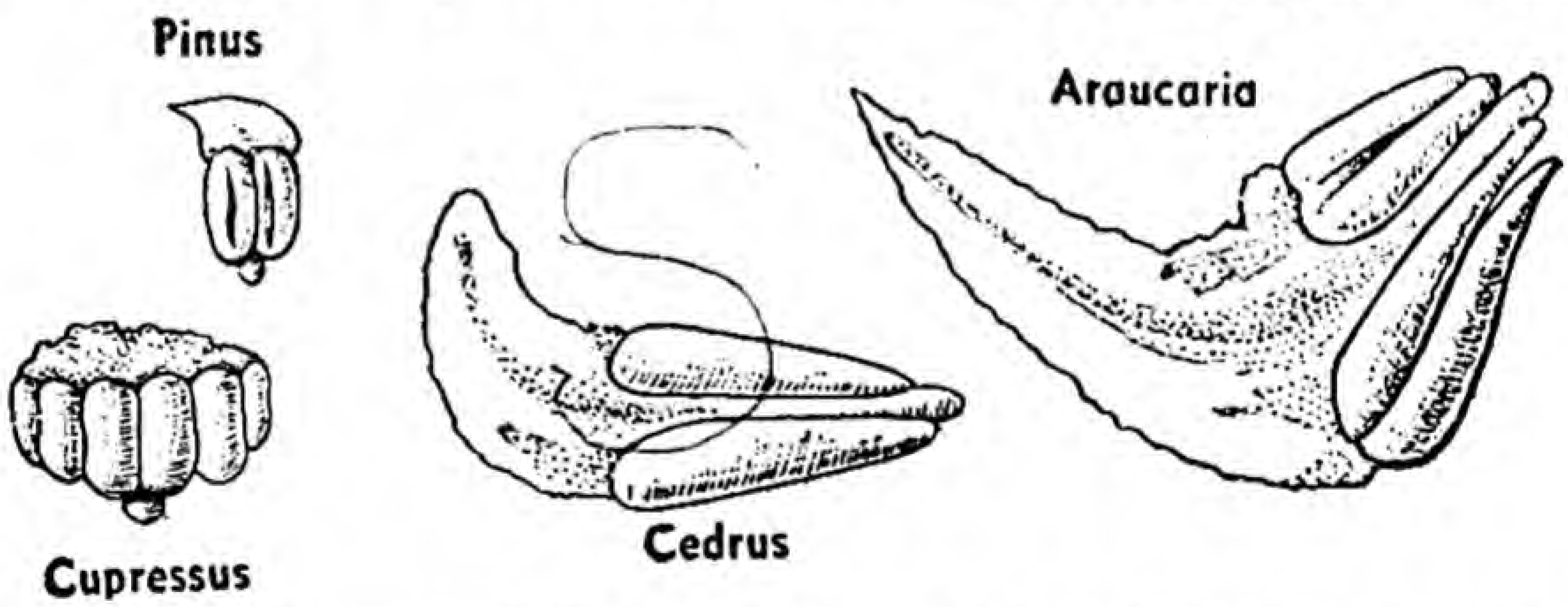


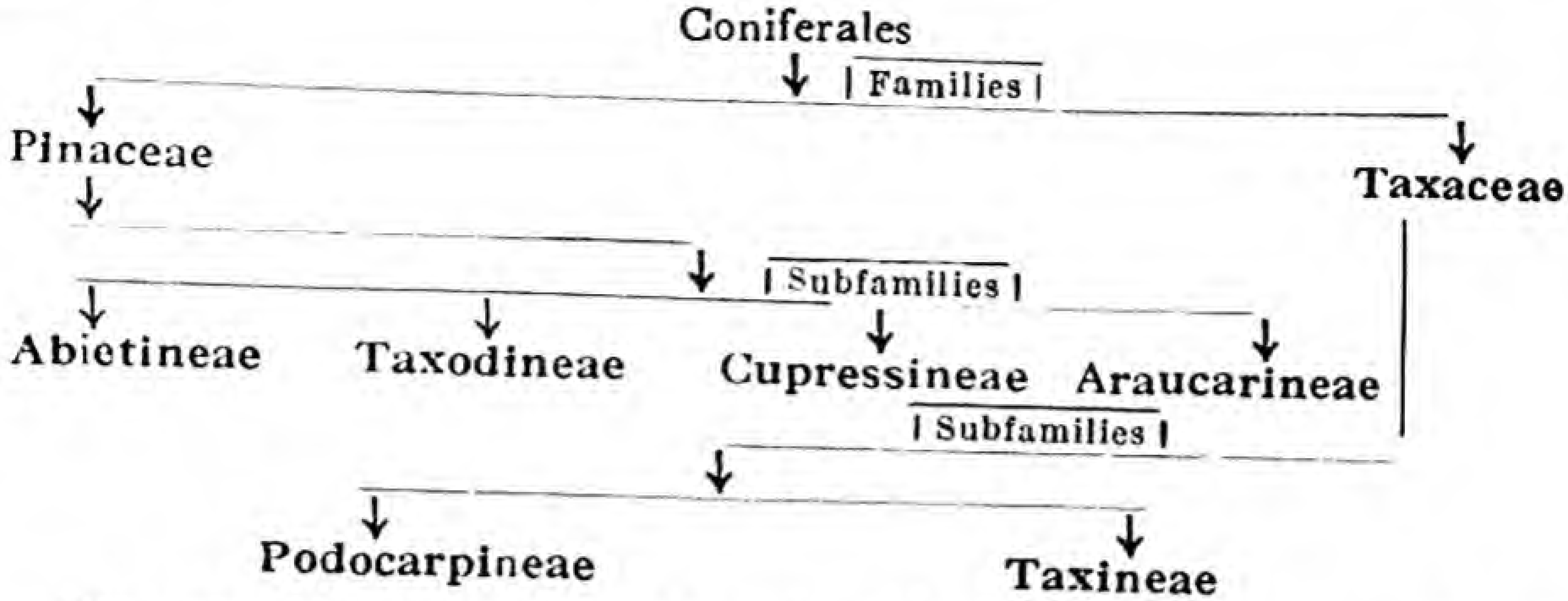

Fig. 7—1 Microsporophylls and microsporangia in some conifers (After Chamberlain).

gametophyte is much reduced, it is retained inside the megasporangium and remains completely dependent on the sporophyte. Male gametes are nonflagellate. Seeds are winged or unwinged, endospermous, nut-like and enclosed in a testa. Polyembryony is prevalent. Cotyledons are two to many and germination is epigeal (fig. 7-33).

CLASSIFICATION—Coulter and Chamberlain[1] divide the Coniferales into two families namely the Pinaceae and the Taxaceae

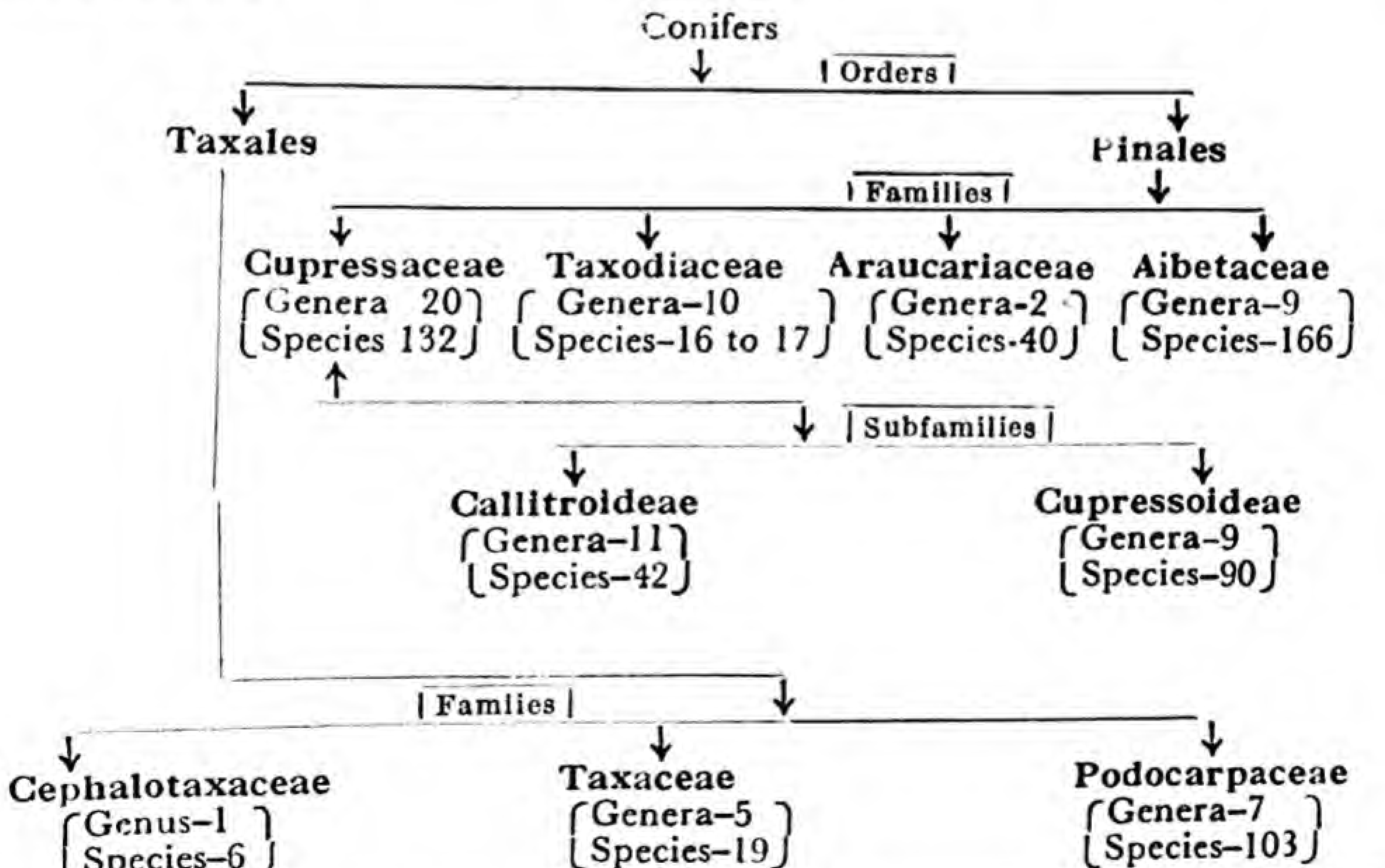
1. Coulter, J. M. and C J. Chamberlain 1910.

Each of these is further subdivided into different subfamilies as below :




Pilger[1] divides the order Coniferales into seven families namely, Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae, Taxodiaceae and Cupressaceae. Chamberlain[2] includes only six families within the Coniferales ; all the above families are listed there except the Cephalotaxaceae which finds no place in his classification.

Hui-Lin Li[3] has divided the conifers into two separate orders namely the Taxales and the Pinales. His classification is given below :




1. Pilger. R. 1926.
2. Chamberlain, C. J. 1935.
3. Hui-Lin Li 1952.

DISTINGUISHING FEATURES OF THE FAMILIES—
1. **Pinaceae (=Abietaceae).** It comprises ten genera including the newly established genus *Cathaya* Chun & Kwang. The family is represented by large resinous trees (fig. 7-2 & 3). Branches are mostly whorled, leaves are evergreen but deciduous in *Larix*. Leaves are stiff, acicular, or linear, they are distichous or arranged in usually 1 to 7 foliate fascicles (fig. 7-4 & 5). Plants are monoecious. Microsporophylls or stamens and ovuliferous scales are spirally arranged round a common axis in the strobilus. The strobili are terminal or lateral. ~~Female~~ ♂ cones possess numerous microsporophylls each possessing two microsporangia (fig. 7-1), with numerous two-winged pollen grains. Female cones with numerous, spirally arranged bract-scales, bearing on their upper surface the more or less free ovuliferous scale; ovules two, anatropous. Seeds mostly unilaterally winged, cotyledons 3 to 18. The genera included in the family are *Pinus* Linn. (80 spp.), *Tsuga* Carr. (10 spp.), *Picea* Diet (10 spp.), *Abies* Miller. (40 spp.), *Cedrus* Trew. (4 spp.), *Larix* Miller (11 spp)., *Pseudotsuga* Carr. (6 spp.), *Keteleeria* Carr. (4 spp.), *Pseudolarix* Gord. (1 sp.) and *Cathaya* Chun & Kwang (1 sp.)

2. **Taxodiaceae**—It is represented by large trees, leaves are narrow ; scaly, needle or sickle-shaped. Plants are monoecious. Male flowers are either solitary, terminal or lateral, capitate or in panicled inflorescence. Microsporophylls are short, stalked and bear 2 to 8 microsporangia. Dehiscence of anthers is by longitudinal slits. Pollen grains are unwinged. Female cones solitary, terminal ; bract and ovuliferous scales numerous, partly or completely fused; ovules 2 to 9, erect or anatropous. Female strobili are globose or ovoid ; leathery or woody. Seeds are dry with woody shells, they are winged but wings are short. Cotyledons are 2 to 9. The family includes 9 living genera namely, *Taxodium* Rich. (3 spp)., *Crytomeria* D. Don (1 to 2 spp.), *Sciadopitys* Sieb. et Zucc. (1 sp.), *Sequoia* Endl. (1 sp.) *Metasequoia* Miki (1 sp.), *Cunninghamia* R. Br. (2 spp.), *Athrotaxis* D. Don (3 spp.), *Glyptostrobus* Endl. (11 spp.) and *Taiwania* Hayata (2 spp.), this is represented in northern Burma by *T. cryptomerioides* Hayata. A species of *Sequoia* viz., *S.*

*giganteum* (Lindl.) Buchholz has been raised to generic rank, *Sequoiadendron*[1] Buchholz,

3. **Cupressaceae**—It is represented generally by small trees or shrubs. Leaves are small, scaly, decussate or in whorls closely appressed to the branches. Cone-scales opposite or in whorls of three. Female strobili are small in size. Ovuliferous scales are thin or fleshy. Stamens possess short filaments, connective is prolonged into a peltate scaly appendage. Anthers 2 to 6 are globose in form. Ovules are few to many, sessile and orthotropous. They are borne at the base of the scale, or 1 to 3 ovules may be terminal as in *Juniperus*. The ripe cone consists of woody or fleshy scales. Seeds are solitary but sometimes they are numerous.

The family includes about 21 genera, the chief being *Callitris* Vent. (16 spp.), *Widdringtonia* Endl. (5 spp ), *Thuja* L. (5 spp.), *Libocedrus* Endl. (5 spp.), *Cupressus* L. (15 to 20 spp)., *Chamaecyparis* Spach. (7 spp.) and *Juniperus* L. (60 spp.) Others are *Tetraclinis* Mast (1 sp.), *Actinostrobus* Miq. (2 sp.) *Neocallitropsis* Florin (=*Callitropsis* Compt.) (1 sp)., *Fitzroya* Hook. f. (1 sp.), *Diselma* Hook. f. (1 sp.), *Thujopsis* Sieb. & Zucc. (1 sp.), *Fokienia* A. Henry & H. H. Thomas (1 to 3 spp.).

*Cupressocyparis* Dallimore is a hybrid between *Cupressus macrocarpa* and *Chamaecyparis nootkatensis*. *Papuacedrus* Li has 3 spp., *Octoclinis* F. Muell—1 sp., and *Heyderia* C. Koch.—1 sp.; *Arceuthos* Ant. & Kotschy—1 sp. (=*Juniperus drupacea* Lab.), *Pilgerodendron* Florin 1 sp., (=*Libocedrus tetragona* Endl.), and *Biota* Endl. 1 sp. (=*Thuja orientalis* L.)

4. **Araucariaceae**—It is represented by tall trees possessing awl-shaped leaves. Strobili are large in size. Scales are completely fused with sporophylls. Several prothallial cells occur in the male gametophyte and several archegonia occur in the female gametophyte. The family includes only two genera namely, *Agathis* Salisb. (20 spp.) and *Araucaria* Jussieu (20 spp.)

5. **Podocarpaceae**—It is represented by evergreen shrubs or large trees possessing elliptic, linear or lanceolate, spirally arranged

1. Buchholz J. T. 1931

leaves which vary in size from small scales to nearly 30 cm in length. Young leaves are red in colour. Plants are dioecious. Male strobili are cylindrical, dense, catkin-like, axillary or terminal in position. Stamens are numerous and filaments short. Pollen grains are two-winged. Ovules are stalked or sessile; axillary or terminal in position with usually 2 to 4 scales, one or two of which bear in their axils a fertile scale called the epimatium which is folded over and partially fused with an inverted ovule. Seeds are round or ovoid. The family includes 7 genera namely, *Acmopyle* Pilger (3 spp.), *Podocarpus* L Hérit ex. Pers. (70 spp.), *Dacrydium* Solander ex Forst. (20 spp.), *Microcachrys* Hk. (1 sp.). *Pherosphaera* Archer (2 spp.), *Saxegothaea* Lindl. (1 sp.) and *Phyllocladus* Rich. (6 spp.). *Podocarpus imbricatus* R. Br. and *P. neriifolius* D. Don. occur in Burma and Eastern Himalayas while *P. wallichianus* C. Presl (= *P. latifolius* Wall.), occurs in Assam and South India.

6. **Cephalotaxaceae**—It is represented by shrubs or small dioecious trees. Ovuliferous shoot is quite reduced. Leaves are similar to *Taxus* in their linear, flat shape and alternate arrangement but possess resin canal on the lower side. Male strobili 6to11, forming globose heads; they arise in the axil of membranous bracts and are supported by a single involucre of imbricating scales. Female strobili are small and pedunculate. Each strobilus consists of 6 to 20 scales, each of which possesses two ovules at the base, but only one seed appears to be enclosed in a fleshy cup. Seeds are large in size. The family includes a single genus *Cephalotaxus* Siebold and Zucc. with 6 species two of which namely, *Cephalotaxus mannii* Hk. and *C. griffithii* Hk. occur in Assam.

The conifers have a long and continuous history extending from the carboniferous to the present day. At one time they formed the dominant vegetation of the earth. The fossil conifers are usually kept in distinct families indicated below :

(i) Lebachiaceae with *Lebachia* (fig. 7-24 A), *Ernestiodendron* (fig. 7-24 B), *Walchia*, *Walchiostrobus*, *Carpentieria* and *Buriadia*

(ii) Voltziaceae with *Pseudovoltzia* (fig. 7-24 H), *Voltziopsis*, *Ullmannia* (fig. 7-24 F & G) and *Voltzia*
(iii) Palissyaceae with *Palissya* and *Stachyotaxus*
(iv) Cheirolepidaceae with *Cheirolepis*, *Indostrobus* and *Takliostrobus* etc.

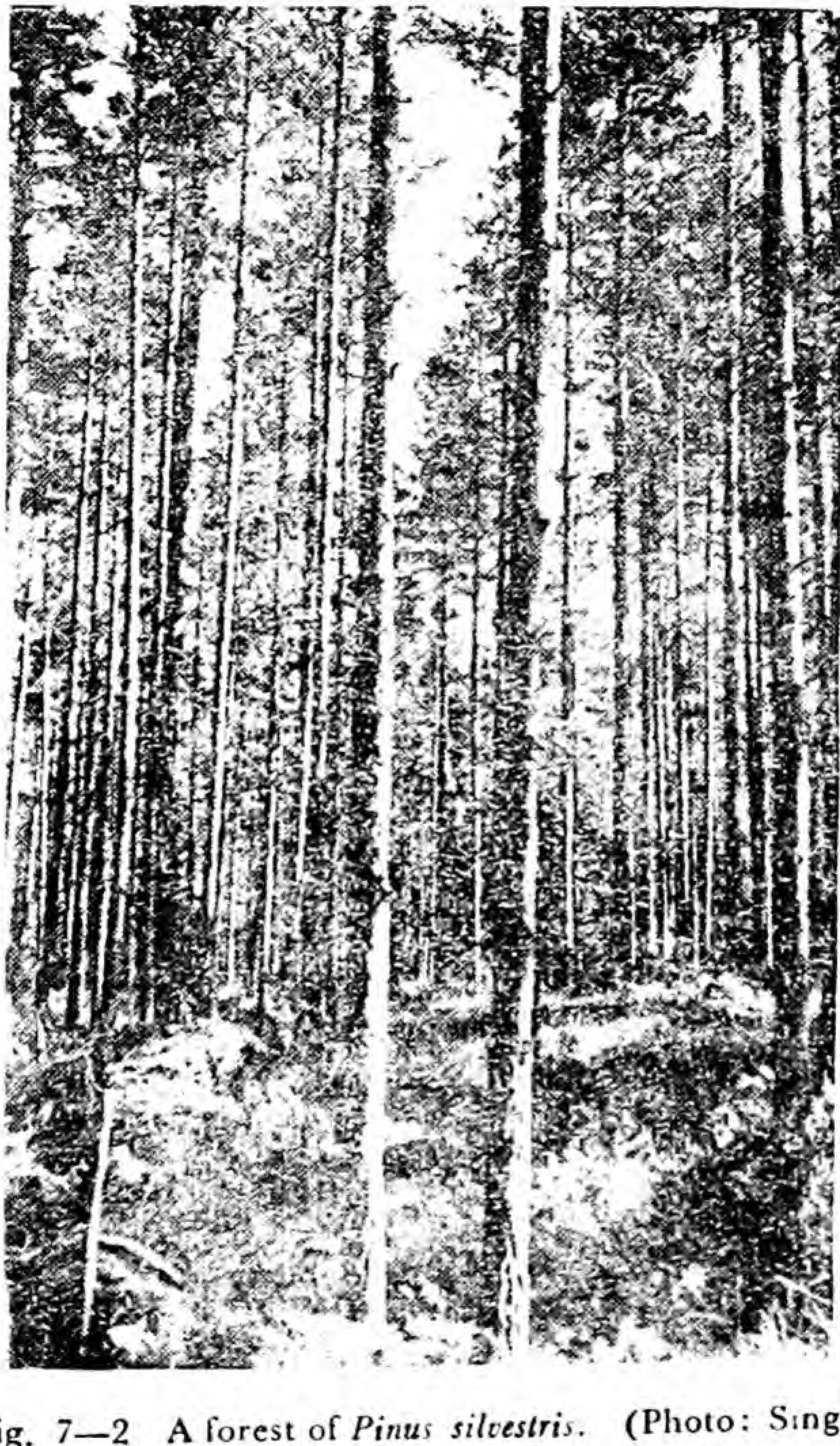


Fig. 7—2 A forest of *Pinus silvestris*. (Photo: Singhal)

Some of the coniferous remains, known from India, which can be satisfactorily placed in some of the families indicated above are : *Brachyphyllum* Brongn., *Pagiophyllum* Heer, *Mohgaostrobus* Prakash, *Conites* Sternberg, *Coniferocaulon* Seward and many wood-genera such as *Dadoxylon*, *Barakaroxylon*, *Prototaxoxylon* etc., and the leaf-genus *Desmiophyllum* ( = *Podozamites*) *indicum*.

## *PINUS* Linn.

SYSTEMATIC POSITION—

Order—*Coniferales*

Family—*Pinaceae*

Genus—*Pinus* Linn.

GEOGRAPHICAL DISTRIBUTION OF THE INDIAN SPECIES—*Pinus*, the most dominant genus of the order, is represented by nearly 90 species. It forms an evergreen forest belt in the north temperate and arctic regions (fig. 7-2). It is widely distributed in the hills and is an important source of timber and resin. In India the genus is represented by six species which grow in the North-East and the North-West Himalayas (fig. 7-3). *Pinus* does not grow in wild state in the hills of South India but is planted there. The only conifer that occurs in South India in the wild state is *Podocarpus wallichianus.*

DISTINGUISHING FEATURES—On the basis of the number and the form of leaves the six species of *Pinus* which occur in India can be identified as below[1]:

Leaves in fascicles of 5, sometimes slightly bent (fig. 7-5) *P. wallichiana.* A. B. Jacks.

Leaves in fascicles of 5, usually sharply bent 1.3 cm to 2.0 cm from base *P. armandi* Franchet

Leaves in fascicles of less than 5

Leaves 3 in a fascicle

Leaves stiff, less than 15.5 cm long *P. gerardiana Wall.*

Leaves soft more than 15.5 cm long

Wings four times as long as the seed;

Umbo of scales with a prominent beak – *P. insularis Endl.*

Wings about the length of the seed;

Umbo of scales with a prominent hooked beak ... *P. roxburghii* Sarg.

Leaves only 2 in a fascicle ... *P. merkusii* Junghet DeVriese

1. Raizada, M. B. and K. C. Sahni 1960.

Characters of the six species of *Pinus* that occur in India are enumerated below:

(1) *P. gerardiana* (the Chilgoza pine) possesses needle-like leaves, 3 in number. Tree attains a height of nearly 18 metres. Seeds measure about 2.5 cm in length and are edible. These are commonly called 'chilgoza'. The wing of the seed is small and deciduous. It grows in Kashmir, West Pakistan and Afghanistan and Kinnaur District of Himachal Pradesh, where rainfall is scanty but winter snowfall is heavy. It grows luxuriantly between an altitude of 2100 to 3300 metres (fig. 7-3).

(2) *P. merkusii*. (the Tenasserim pine) possesses needle-like leaves two in number. It hardly reaches a height of 3 metres and grows profusely on hillocks in Burma, East India, Bengal etc., coming down even to an altitude of 150 metres (fig. 7-3).

(3) *P. roxburghii* [=*P. longifolia* Roxb.] (the Chir pine) possesses needle-like leaves three in number. The trees are pyramid-like, large in size and grow all along the Himalayas between the altitude of 450 to 2250 metres (fig. 7-3 & 7-4). Leaves are 12 to 20 cm long and triangular in cross section. It is commonly known as 'chir', and grows in abundance in the hills of West Pakistan, Kashmir, Punjab, Himachal Pradesh, Nepal and Uttar Pradesh. It may attain a height of nearly 54 metres and the stem may be 3 metres in girth. Its seeds are also edible.

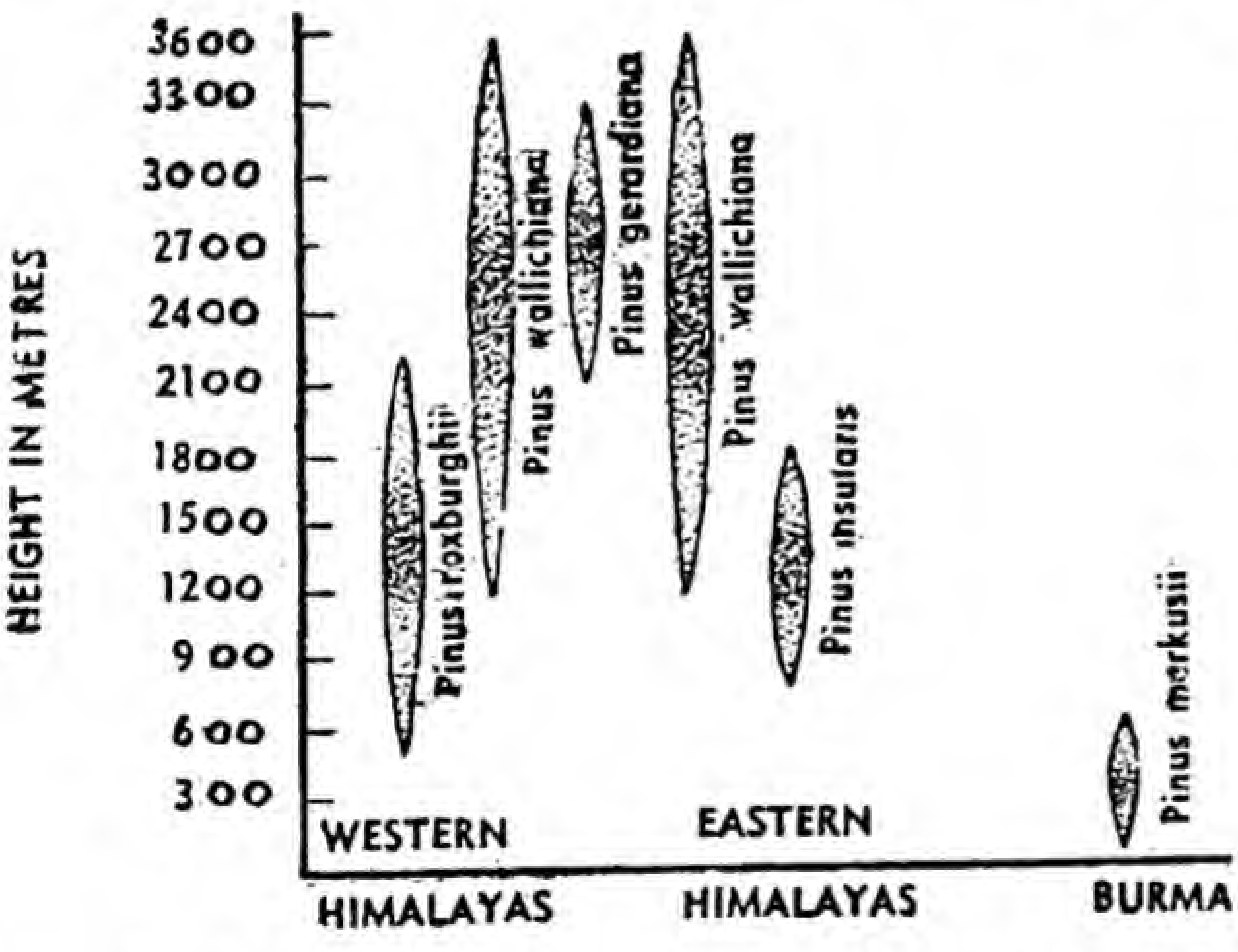



Fig. 7—3 Altitudinal distribution of the different species of *Pinus* growing in the Himalayas and Burma (After Konar).

(4) *P. wallichiana* [=*P excelsa* Wall.] (the blue pine) possesses needle-like leaves, five in number (fig 7-5). It is an evergreen tree with glaucous, bluish foliage. The tree may attain a height of 5

metres under favourable conditions. Female strobili are cylindrical in shape. It commonly occurs between an altitude of 1800 to 2100 metres (fig. 7-3) and grows luxuriantly in areas with an annual rainfall of 90 to 200 cms. It is commonly called 'Kail'. The strobili are pendulous without any pronounced beak on the apophysis. It grows in the hill-ranges of West Pakistan, Kashmir, Himachal Pradesh, Punjab, Nepal and Bhutan.

(5) *P. insularis.* [=*P. khasya* Royle] (the Khasi Pine) possesses needle-like leaves, three in number. It grows in abundance in the hill ranges of Assam and Burma. Trees of *P. insularis* are comparatively smaller in size, reaching a height of about 30 metres under favourable conditions (fig. 7-3). The trees are evergreen, possessing whorled branches.

(6) *P. armandi* Franchet (Armand's pine) differs from *P. wallichiana* in the presence of (i) a distinct bend near the base of the leaf, (ii) glands on the young shoots, (iii) stouter strobili and (iv) wider scales. The trees are tall attaining a height of nearly 18 metres. This species occurs in Central and West China, Formosa and North-East frontiers of Assam.

MORPHOLOGICAL FEATURES—*Pinus* is a large tree with evergreen, acicular (needle-like) leaves. The form of the tree is pyramidal due to spiral growth of lateral branches. Some of the trees are quite tall. Plants are monoecious

**Root**—A tap root is present. Root hairs are scanty and an ectotrophic mycorrhiza occurs.

**Stem**—It is cylindrical and is covered with bark which is characteristic of different species. The main stem is called the shaft and is used for timber. Branching is monopodial. Two types of branches occur, namely, the long branches of unlimited growth and short ones (=dwarf or spur-shoots) of limited growth. The spur-shoots develop in the axils of scale leaves and are devoid of apical buds. These possess scale leaves below and needle-like leaves at the apex. Konar[1] states that each dwarf

1. Konar, R. N. 1960.

or spur-shoot in *P. roxburghii* usually bears prophylls and 8 to 10 spirally arranged persistent cataphylls (=scale leaves) which in the beginning are green but later turn brown.

**Leaves**—Mature foliage leaves are needle-like. Their number varies from 1 to 5 in different species; abnormal specimens may have more. On the number of needles that a dwarf or spur shoot possesses, it may be called unifoliar, with one, e.g., *P. monophylla*; bifoliar with two, e.g., *P. sylvestris*. *P. merkusii*; trifoliar with three, e.g., *P. gerardiana*, *P. roxburghii* (fig. 7-4); and pentafoliar with 5 needles, e.g., *P. wallichiana* (fig. 7-5). *Pinus* produces dimorphic (long and dwarf) shoots and dimorphic (needle-like and scaly) leaves. Scale leaves occur on long as well as on short shoots and fall off as the branches attain maturity, but adult leaves (=needles) are borne only on the dwarf shoots. In *P. roxburghii* dwarf or spur shoots are initiated in March-April and these unfold a year later; i.e., the following April. Soon after this, the male strobili also mature and shed their pollen.

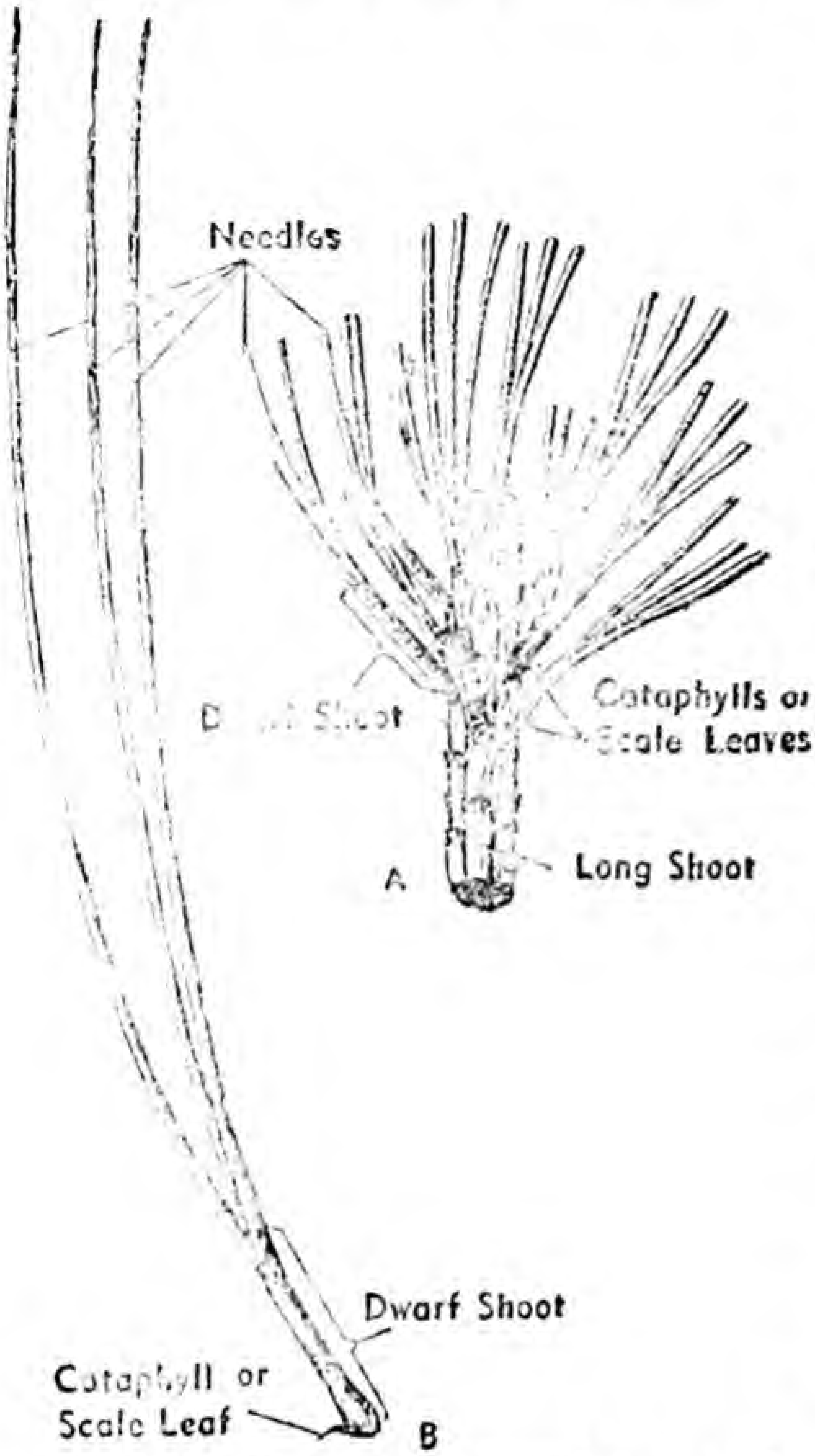



Fig. 7—4 Long and dwarf shoots of *P. roxburghii* with needles and cataphylls A—a long shoot with several dwarf shoots; B—a dwarf shoot, with 3 needles.

HISTOLOGICAL FEATURES—The root of *Pinus*, when young, is surrounded by an outermost piliferous layer, the epiblema, from which arise thin-walled root hairs (fig. 7-6). Even the young roots have few root hairs because of the presence of a fungus on the surface of the root. This is called ectotrophic mycorrhiza. It probably helps in the availability of food. Epi-

blema is followed by multilayered cortex, made up of parenchymatous tissue. Endodermis occurs next to the cortex; it is single layered, this in turn is followed by pericycle which is sometimes several layered thick. Vascular cylinder is diarch to tetrach. Vascular bundles lie opposite the resin canals. Protoxylem is always exarch. It is slightly forked in the form of 'Y'. Often there occurs a resin canal opposite each protoxylem group (fig. 7-7).

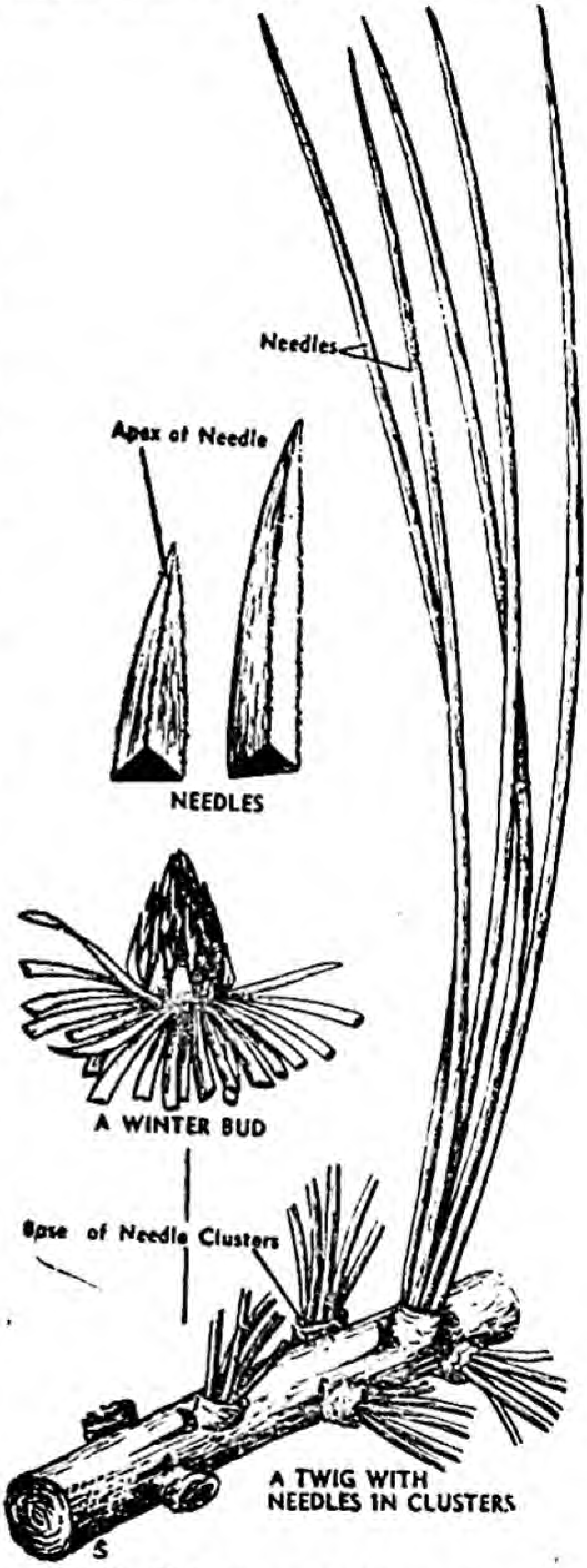



Fig. 7—5 *Pinus wallichiona* showing clusters of 5 needles with their apices and a winter bud (After Dallimore and Jackson).

**Secondary growth of the root**—As the root grows a few cells lying in between xylem and phloem become meristematic and get transformed into cambium. These cells divide and form secondary xylem and secondary phloem on the inner and outer sides respectively., Extrastelar secondary growth takes place like that of a dicotyledonous root by the activity of cork cambium or phellogen, which is formed from the outer layer of pericycle. Phellogen cuts off cork cells or phellem on its outer and phelloderm or secondary ground tissue on its inner sides respectively. Phellem, phellogen and phelloderm together constitute the periderm[1] (fig. 7-7)

The tracheids of the secondary wood of roots are longer and

1. Burns, Mary Anne 1964.

broader and the growth rings narrower in comparisen to those of the stem. Lateral roots emerge from the inner layers of the pericycle. In older roots primary xylem may disappear; then it is difficult to distinguish the root histologically from a stem.

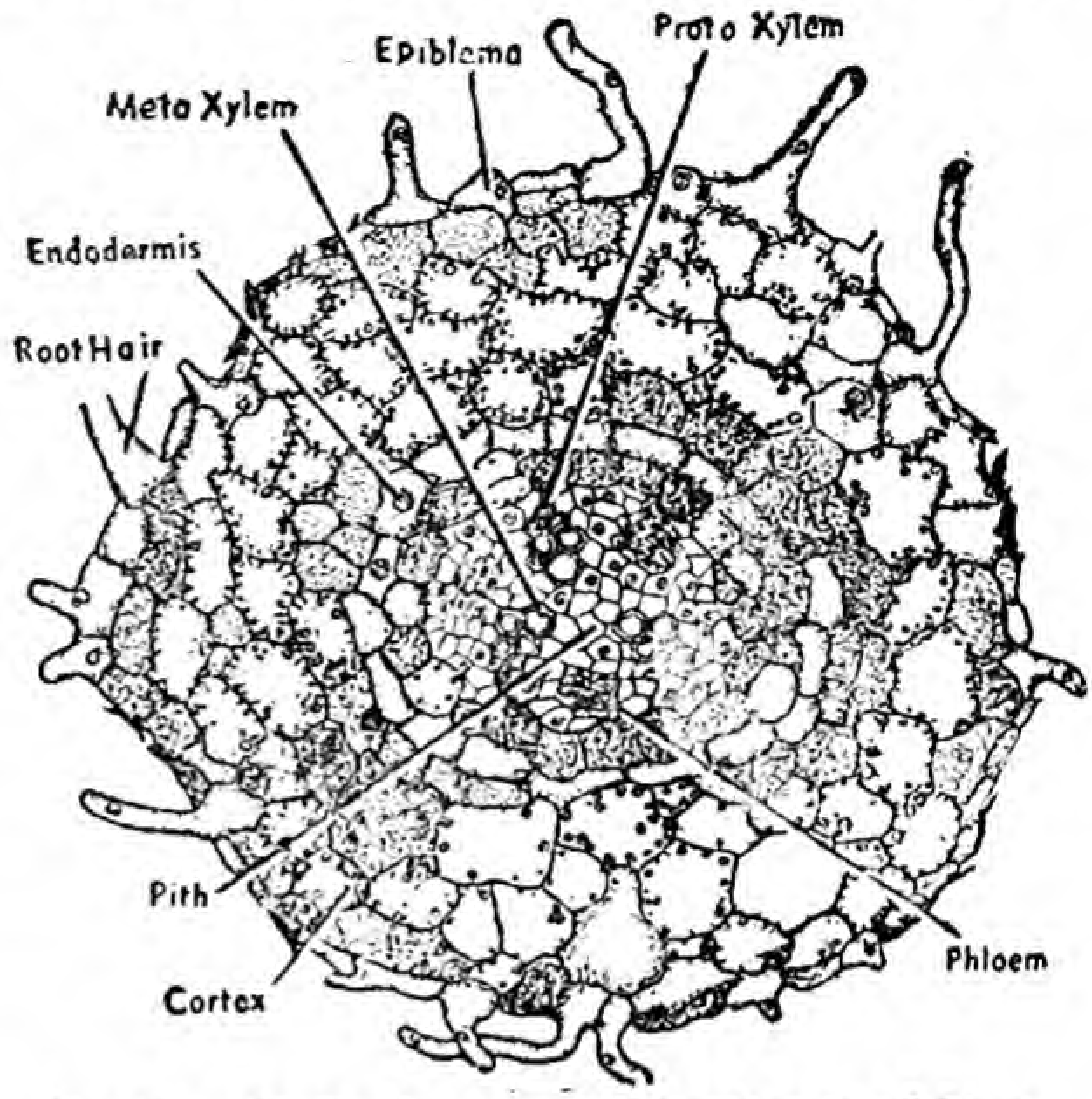



Fig. 7-6 T. S. of a young triarch root of *Pinus*.

A young stem of *Pinus* shows a wavy outline (fig. 7-8) because of the presence of leaf-bases. The stem possesses a thick cuticle below which lies a thick-walled, single-layered epidermis. This layer is followed by multilayered cortex, the outermost layers of which are sclerenchymatous but a few inner ones, in the young stage at least, may be parenchymatous. Resin canals occur in the cortex outside the vascular bundles. The vascular cylinder is eustelic or polyfascicular endarch siphonostelic. Vascular bundles are similar to dicotyledonous stem in their conjoint, collateral and open nature (fig. 7-8). They are arranged in a ring. Xylem rays are narrow and not so wide as in *Cycas* stem. They occur

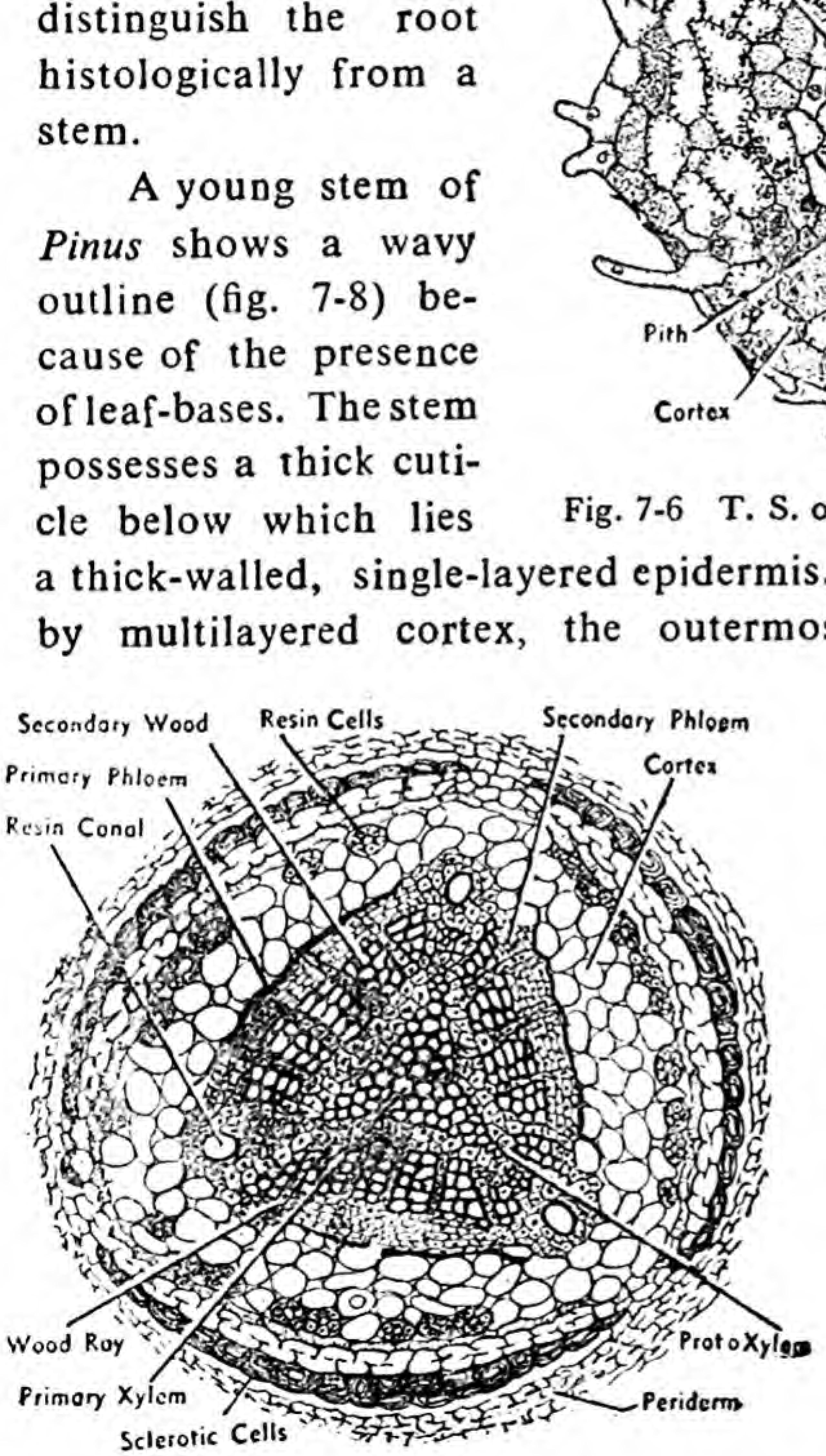



Fig. 7-7 T. S. of an old triarch root of *Pinus* with secondary growth.

in between the vascular bundles and connect the pith with the cortex. Protoxylem is endarch and is made up of tracheids. Phloem consists of sieve cells with sieve plates, phloem parenchyma and albuminous cells. According to Esau[1] the relation between the albuminous cells and sieve cells in the conifers is the same as that between sieve tubes and companion cells in the angiosperms. According to Bierhorst[2] the protoxylem elements possess spiral thickening and bordered pits; rarely annular thickening may also be present. The centre of the stem is occupied by a small pith.

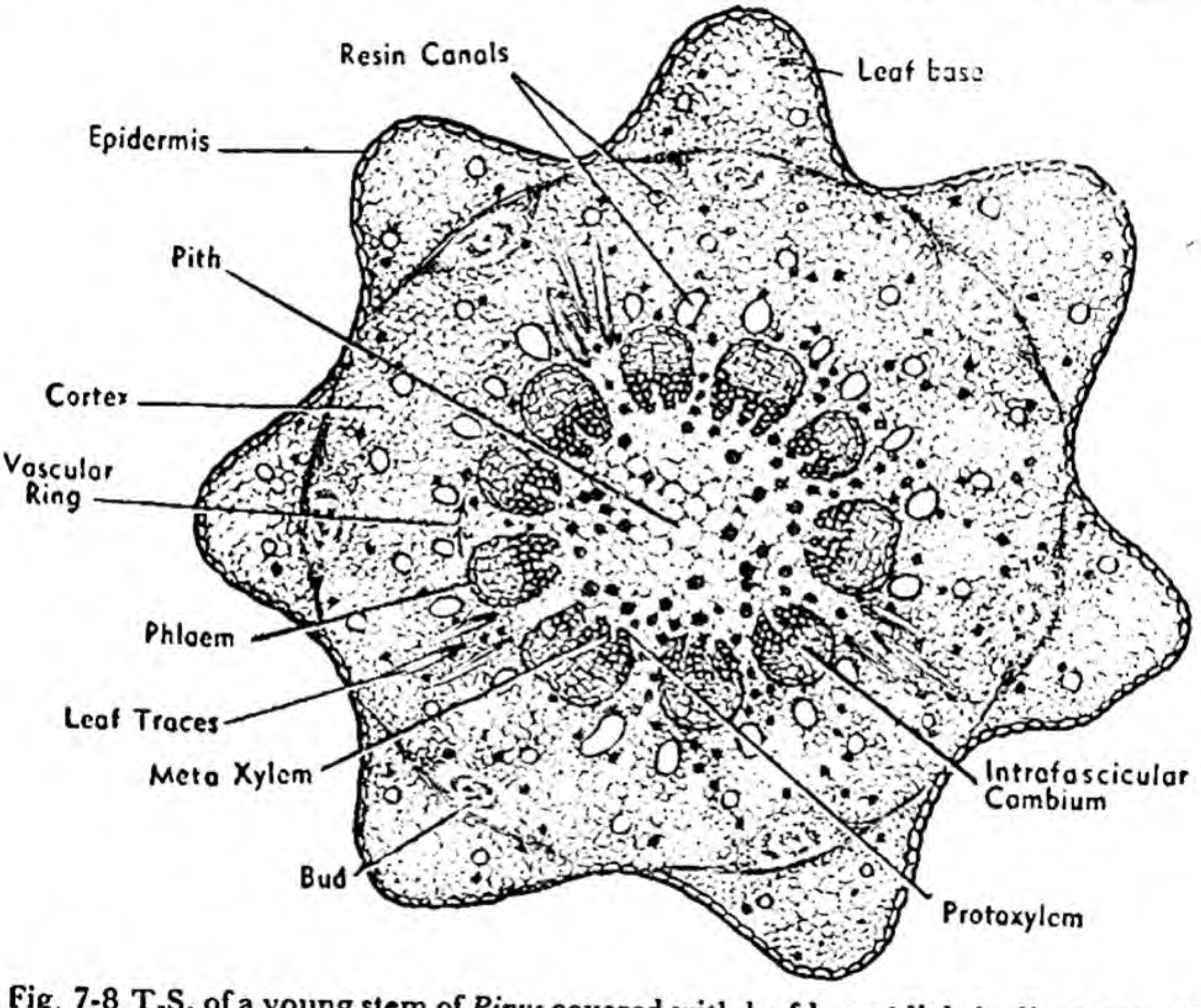



Fig. 7-8 T.S. of a young stem of *Pinus* covered with leaf bases(slightly diagrammatic)

Leaf-gaps are present. In *Pinus* leaf-trace is single at the base, but later it divides into two and is thus regarded as of double nature, a character which is considered to be a primitive one.

**Secondary growth of the stem**—The cambium present in the vascular bundles initiates secondary growth as the stem becomes somewhat old. The cambium forms secondary xylem on its inner and secondary phloem on its outer

1. Esau, K. 1953.
2. Bierhorst, D. W. 1960.

sides. These zones are traversed by xylem rays which too develop from cambium. The secondary wood in *Pinus* shows well-marked growth rings (fig. 7-9). Each ring possesses thin-walled

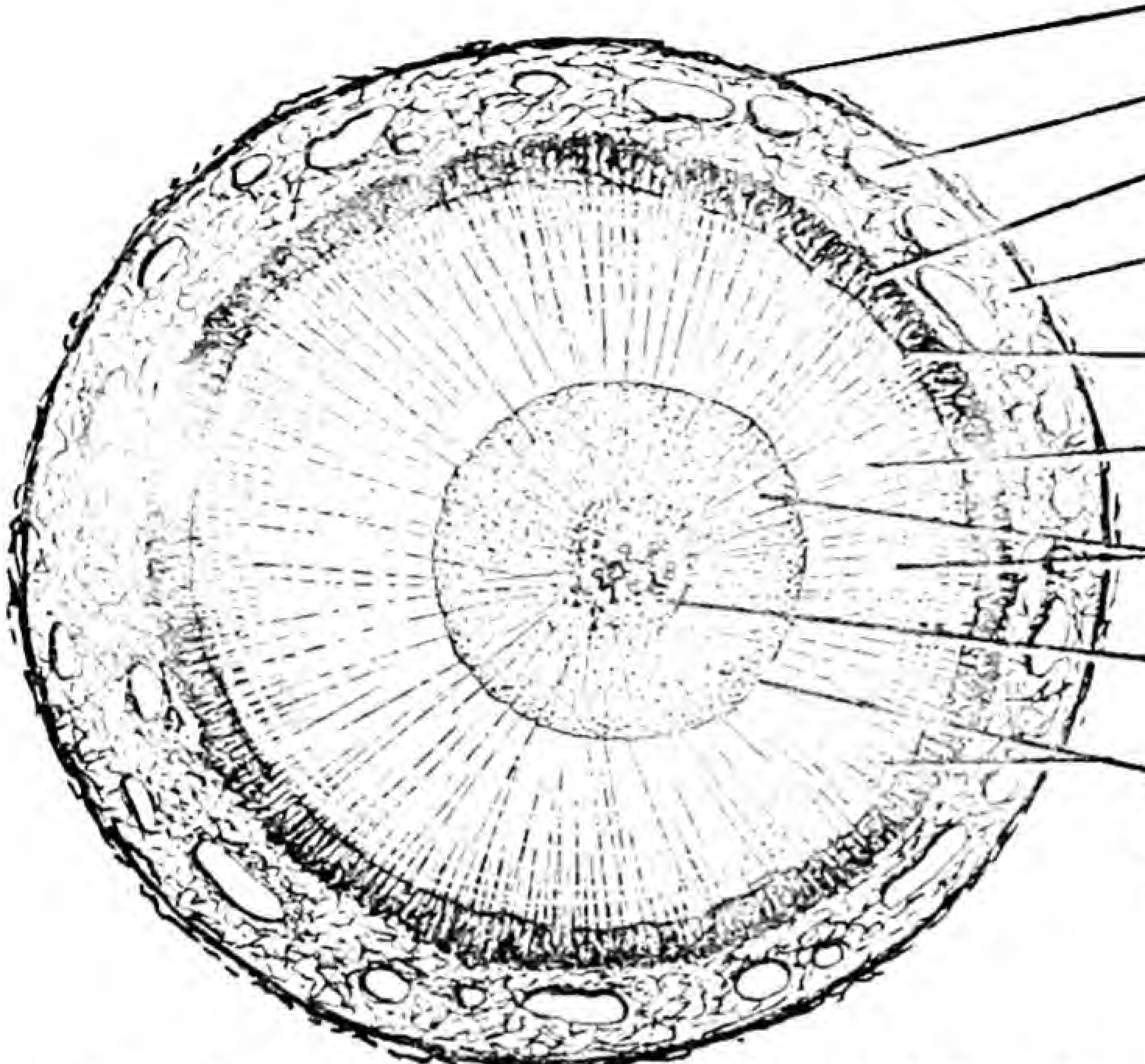



Fig. 7—9 T. S. of a two-year old stem of *Pinus* with growth rings and pycnoxylic wood (After Foster).

spring wood with wide tracheids and large bordered pits. The autumn wood has thick-walled narrow tracheids and small bordered pits (fig. 7-10).

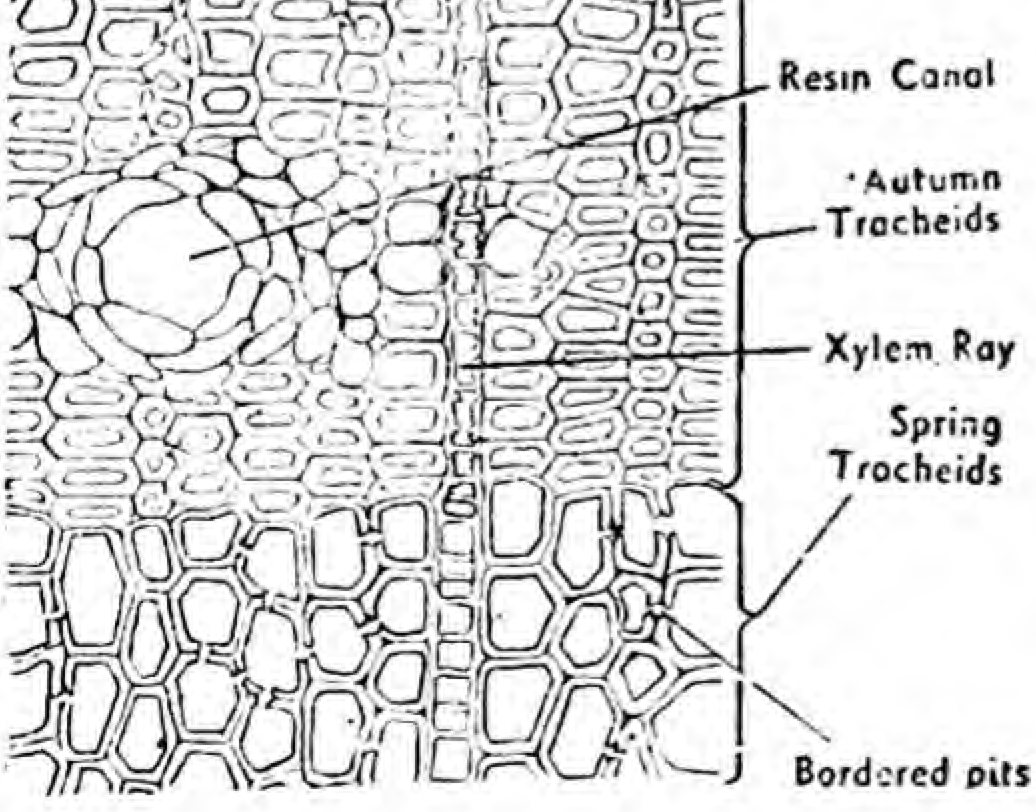



Fig. 7—10 T. S. of the secondary wood of *Pinus* with a resin canal, spring and autumn tracheids (After Wettstein).

Secondary wood is made up of tracheids traversed by xylem rays. The tracheids developing in the spring season are polygonal in transverse section, they have a thinner wall with less lignification than those of the autumn season which are squarish in outline and have a greater deposit of lignin (fig. 7-10 & 7-11). Resin canals are also present in the secondary wood

(figs. 7-10, 7-11 and 7-14 G). Similar to cambium there develops a meristematic layer in the cortex called the phellogen or cork cambium. It cuts off phellem or cork on its outer and phelloderm on its inner side. The cork forms the bark for the protection of stem which in old stems peels off. The tracheids of *Pinus* have bordered pits on their radial and tangential walls (fig 7-12, 7-13 & 7-14 A to E). A bordered pit is a circular area consisting of thin middle lamella overarched on each side by a dome formed by the inner lignified layers of cell wall. The dome possesses an opening in the centre. On the lamella and in between the two

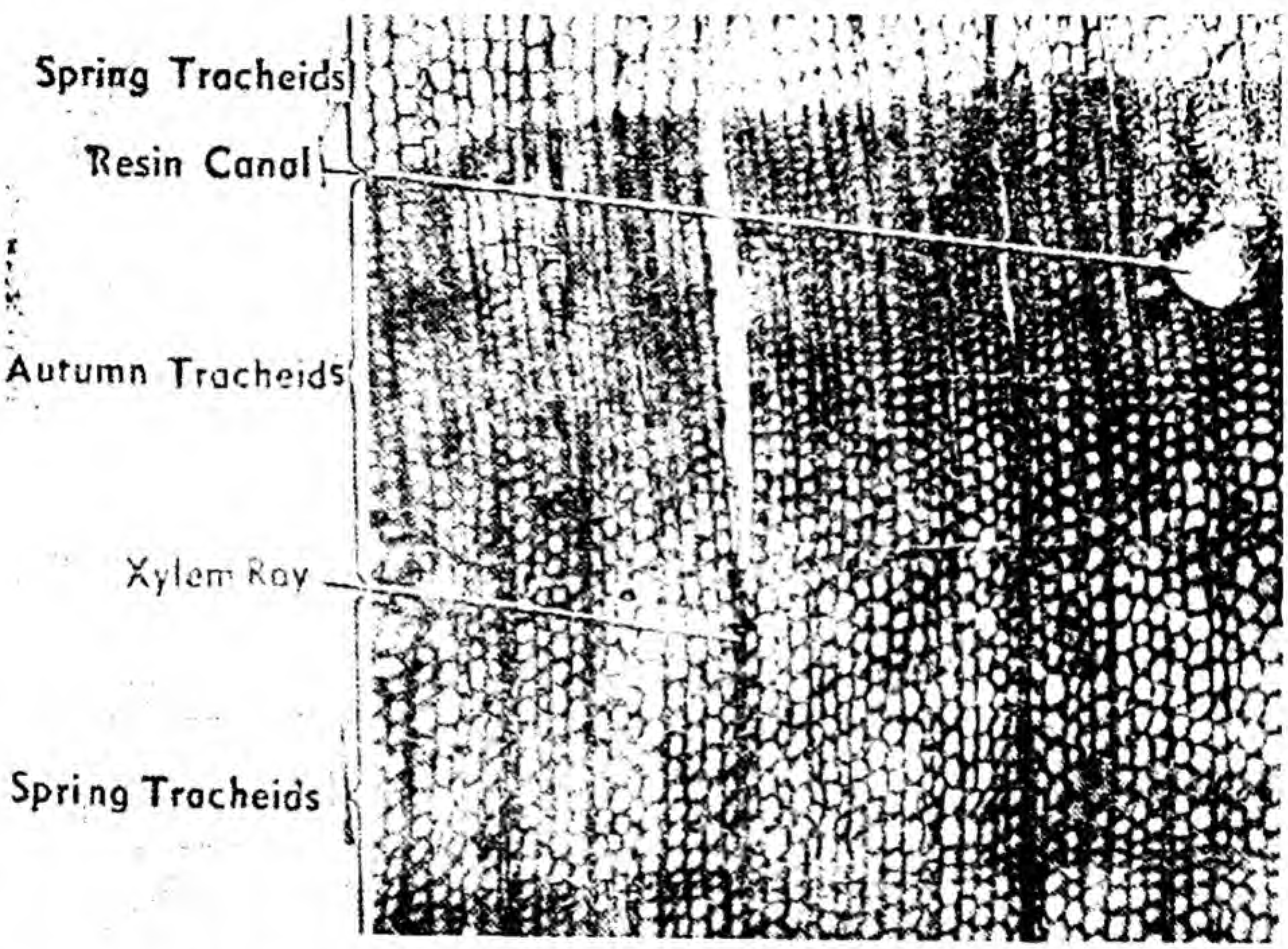



Fig. 7—11 Photo showing the T. S. of the secondary wood of *Pinus*.

openings occurs a small disc of lignin called 'torus' (fig 7-12 C & 7-13). Bordered pits are uniseriate in *Pinus*. Special thickenings of primary lamella surrounding bordered pits called bars or rims of Sanio or crasullae are also present (fig. 7-12 & 7-14). When the pits are too close to each other the pairs of bars of Sanio or crassulae are seen round the rims (fig. 7-12). The walls of resin canals are surrounded by epithelial cells and they are full of resin. Resin canals also occur in association with the multiseriate xylem rays (fig 7-12 C & 7-14 G). In old stems of *Pinus*, annual rings can be clearly made out (fig. 7-9).

The phloem in *Pinus* is made up of radial rows of long sieve cells which taper on both ends. Sieve plates occur mostly on the

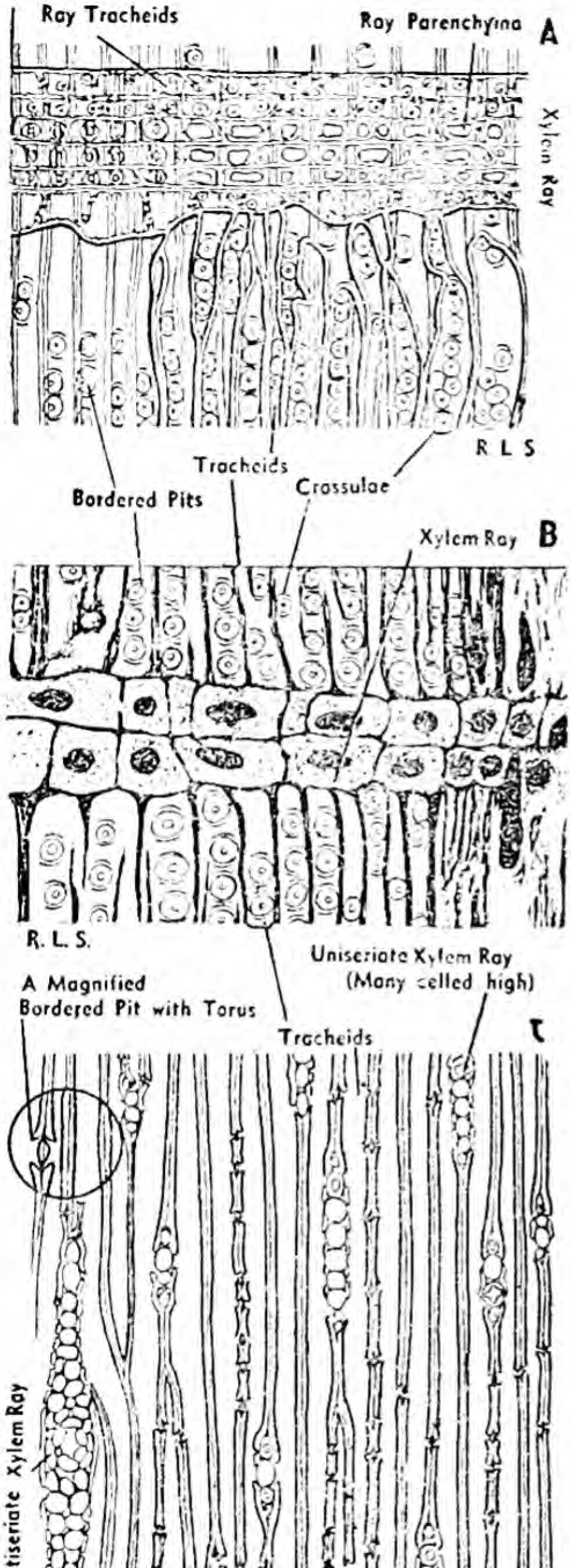



Fig. 17—12 L. S. of the secondary wood of *Pinus*. A—R L. S. (After Wettstein) ; B—R. L. S. showing details of ray parenchyma cells (After Foster); C—T. L. S. (After Wettstein).

radial walls; these may become covered with callus after the first year. There are no companion cells but phloem parenchyma occurs mixed with the sieve cells.

Xylem rays run horizontally and form a closely integrated structure with the vertical system viz., the tracheids and the sieve cells, so much so that every tracheid at least at one point, comes in contact with a living parenchyma cell of the ray. In *Pinus*, the rays are uniseriate in width, but may become multiseriate when they come in contact with a resin canal (fig. 7-12 C & 7-14G). The xylem rays may be only a few cells high or they may be several cells high (fig. 7-12A to C). The marginal cells, on either side of the xylem rays, which are several cells high, get modified into ray-tracheids in the xylem region (fig. 7-12). The ray-tracheids are non-living and have a lignified, thick wall, which may protrude into the lumen of the cells, hence, their walls are irregular in outlines as observed in sections. They are narrower, longer and lower than ordinary parenchyma cells and have bordered pits[1]. In between these cells in the centre of ray are situated the ray parenchyma

1. Eames A. J. & L. H. Mc.Daniels 1947 : 177.

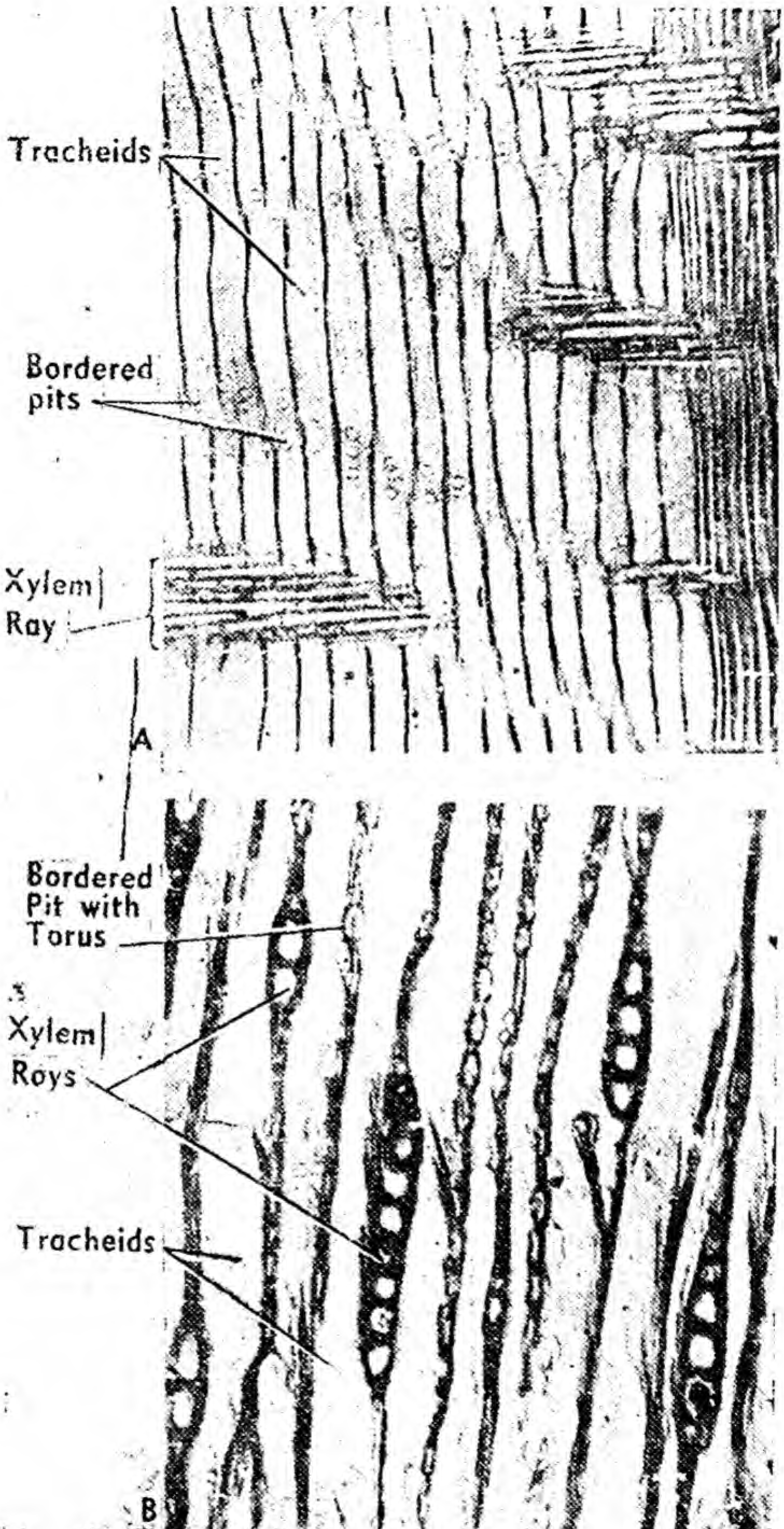



Fig. 7—13 Photo showing the L. S. of the secondary wood of *Pinus* A—R. L. S. & B—T. L. S.

cells which are thin-walled and living and they have simple pits (fig. 7-12A & B). These cells usually store starch.

The xylem ray in the region of the phloem has albuminous cells in position corresponding with marginal ray tracheids. The albuminous cells have smaller transverse diameters than the procumbent ray cells. They have a prominent nucleus and dense contents. They are closely associated with sieve cells and behave like companion cells of the angiosperms. Between the two marginal rows of albuminous cells occur cells of ray parenchyma which unlike the former may have plenty of starch. Thus, the ray in the xylem region has marginal cells which are dead, but it has central cells which are living; in the phloem region, both the cell-layers,

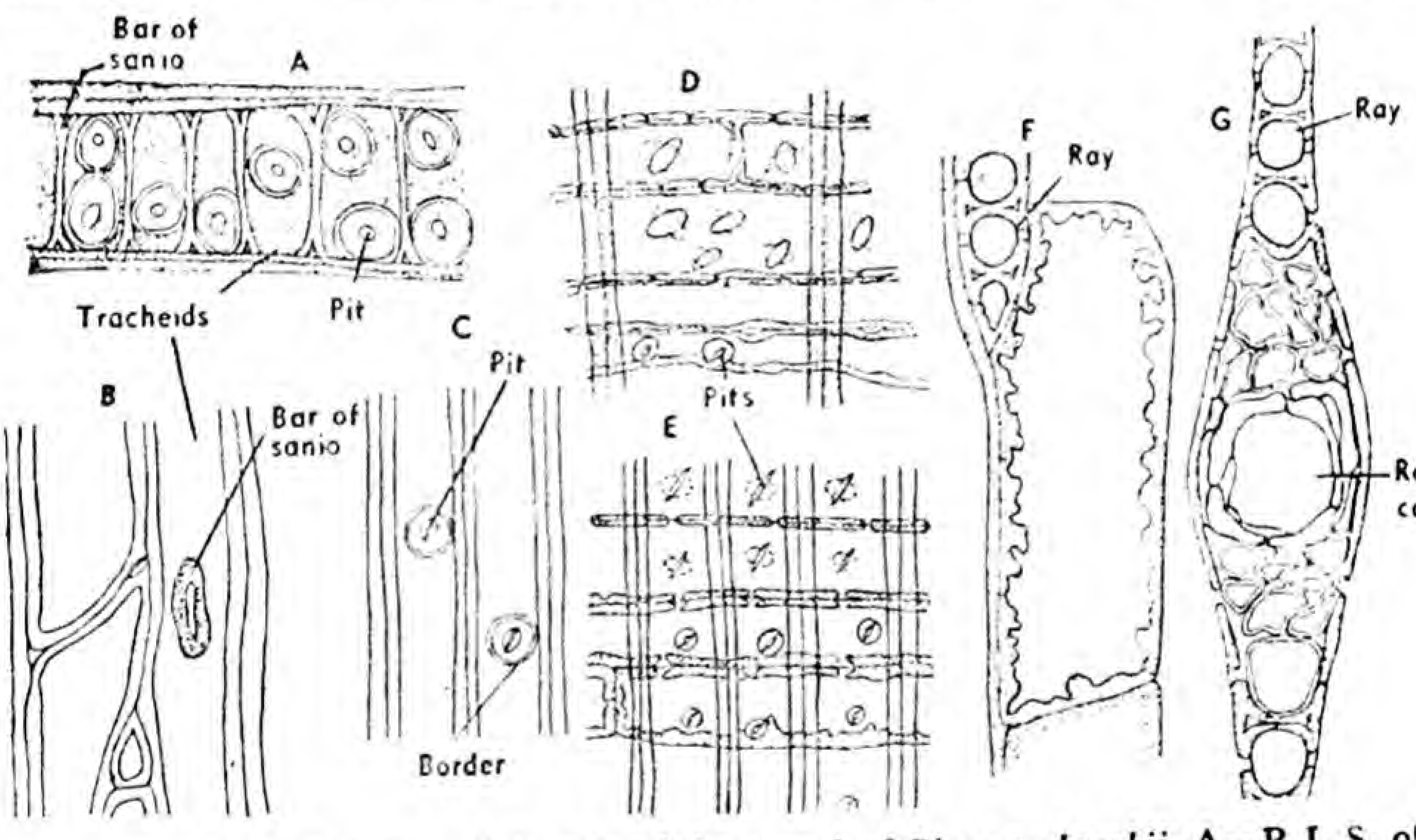
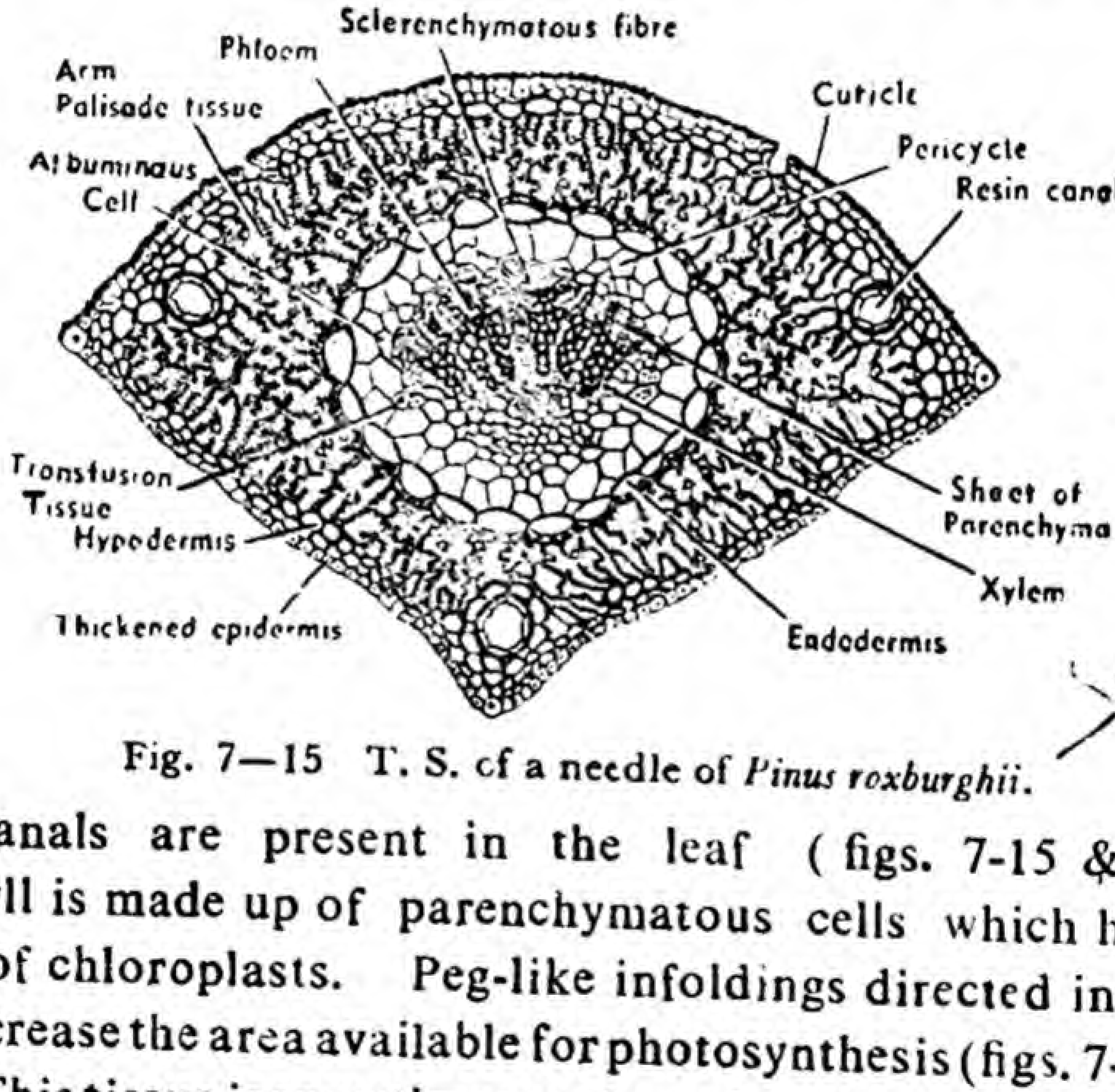



Fig. 7—14 Structural details of the wood of *Pinus roxburghii*, A—R.L.S. of the spring wood showing a tracheid, B—T.L.S. of the wood with a Bar of Sanio in cross section, C—R.L.S. of two summer tracheids, D—R.L.S. of the ray of spring wood, E—R.L.S. of the ray of summer wood, F—T.L.S. of the thick-walled parenchyma adjoining resin duct and ray and G—T.L.S. of a fusiform ray (*After Groom & Ruston*)

marginal as well as the central, are living. According to Bannen[1] the centrally located ray parenchyma cells in the xylem portion of rays and the coextensive starch containing procumbent cells in the phloem part of the rays are apparently the channels of cross transfer and storage sites for carbohydrate assimilates.

1. Bannen, M. W. 1965.

**Leaf**—*P. roxburghii* has three needles in a spur or dwarf shoot (fig. 7-4). They are elongated and long-lived, persisting for 1 to 10 years ; they possess basal meristem. Each needle is triangular in outline possessing two vascular bundles in the centre (fig. 7-15.) The needle of *P. monophylla* has a single vascular bundle. The needle has a single-layered, thick-walled epidermis which is covered with a thick cuticle. Stomata are sunken. Each stoma opens into a respiratory cavity called the vestibule (fig. 7-17 A). Epidermis is followed by a few layers of thick-walled sclerenchymatous hypodermis. This tissue is more developed at the ridges.




Sameena Mehnaz
+ M. Shaila Mahroo

Fig. 7—15 T. S. of a needle of *Pinus roxburghii*.

Resin canals are present in the leaf ( figs. 7-15 & 7-17B ). Mesophyll is made up of parenchymatous cells which have large number of chloroplasts. Peg-like infoldings directed into the cell cavity increase the area available for photosynthesis (figs. 7-15 & 7-17 A & B). This tissue is sometimes spoken of as arm-palisade. The vascular cylinder of the leaf is surrounded by a layer of endodermis made up of barrel-shaped cells (fig. 7-16). This is followed by several-layered parenchymatous pericycle. Pericycle also possesses some sclerenchyma which may form a 'T' shaped girder which separates the two bundles. Abutting on the xylem and extending further are small tracheidal cells with bordered pits; this constitutes the transfusion tissue (fig. 7-16). Occurring near the phloem are parenchymatous cells with proteinaceous contents, called the albuminous cells; these cells have no pits. Thin sheets of paren-

chyma with dense contents, recalling the xylem rays of the stem, extend from the xylem into the phloem. At the base of the needle small amount of cambium may be present.

## LIFE-HISTORY

The adult plant of *Pinus* represents the sporophytic phase. The plants are monoecious, i.e., male and female strobili occur on a single plant. Vegetative reproduction has not been reported. Usually male and female sporophylls are arranged in separate

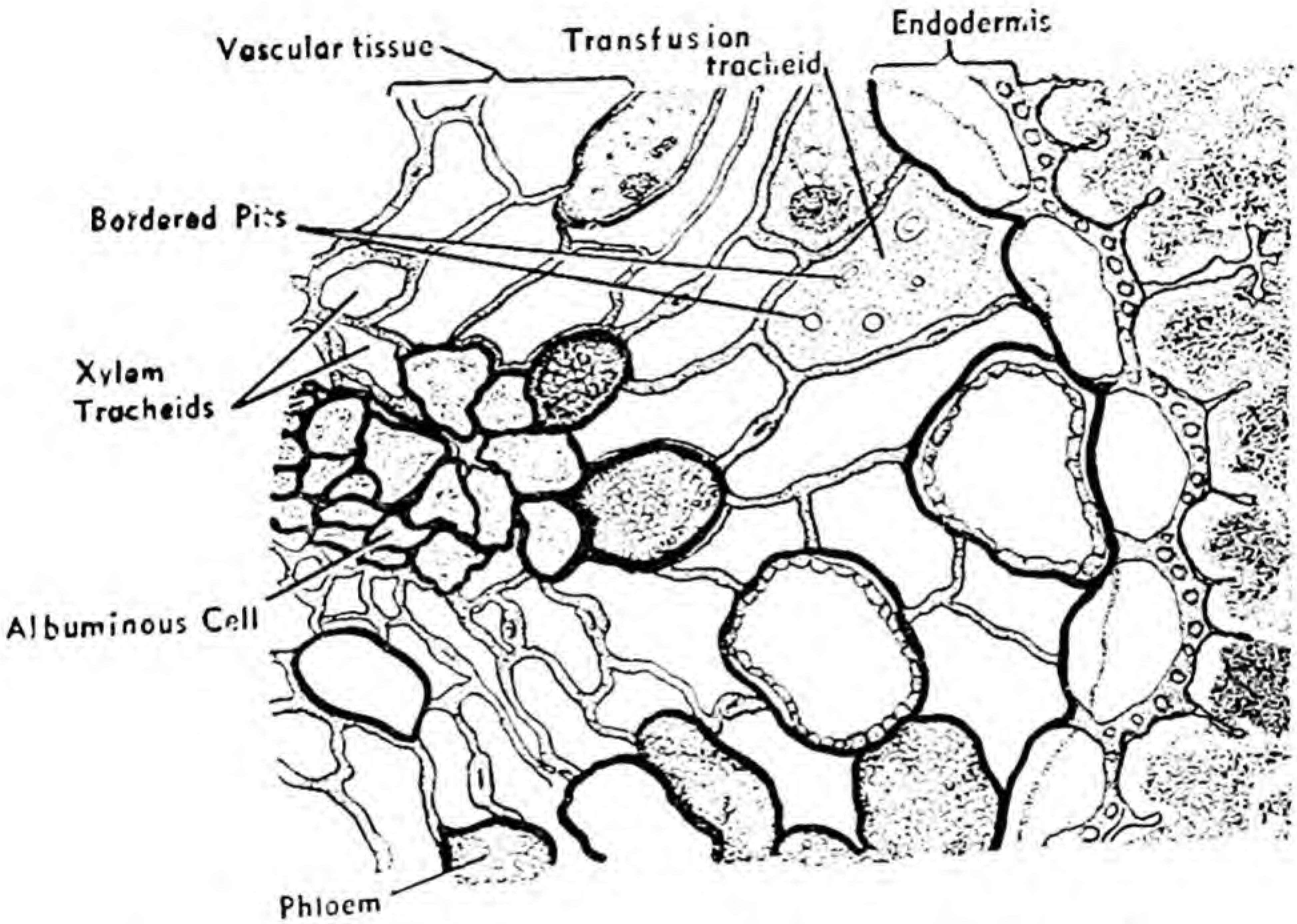



Fig. 7—16 T. S. of *Pinus* needle—highly magnified (After Esau).

strobili but a few abnormal instances are known where micro- and megasporophylls occur mixed together in a single strobilus. Rarely, a few megasporophylls may also be replaced by spurs with needles.

**Male Strobilus**. In *P. roxburghii* clusters of male strobili are initiated in the month of September in Lahore[1] & Delhi.[2] The strobili develop on the shoots of unlimited growth in place of

1. Sethi, M. L. 1929
2. Konar, R. N. 1960.

spur shoots, in the axil of a scale leaf which falls off later (fig 7-18).
Male strobili thus appear to be morphologically equivalent to dwarf shoots. Further, the microsporophylls are borne upon a central axis directly. The male strobilus, therefore, is homologous to the male flower of an angiosperm and not to an inflorescence as is the case with the female strobilus. The central axis of the strobilus corresponds to the thalamus or the torus of an angiospermous flower. In *P. roxburghii* the young male strobilus is externally covered by several bracts, it is about 3 to 4 cm long and 0.64 cm in diameter.

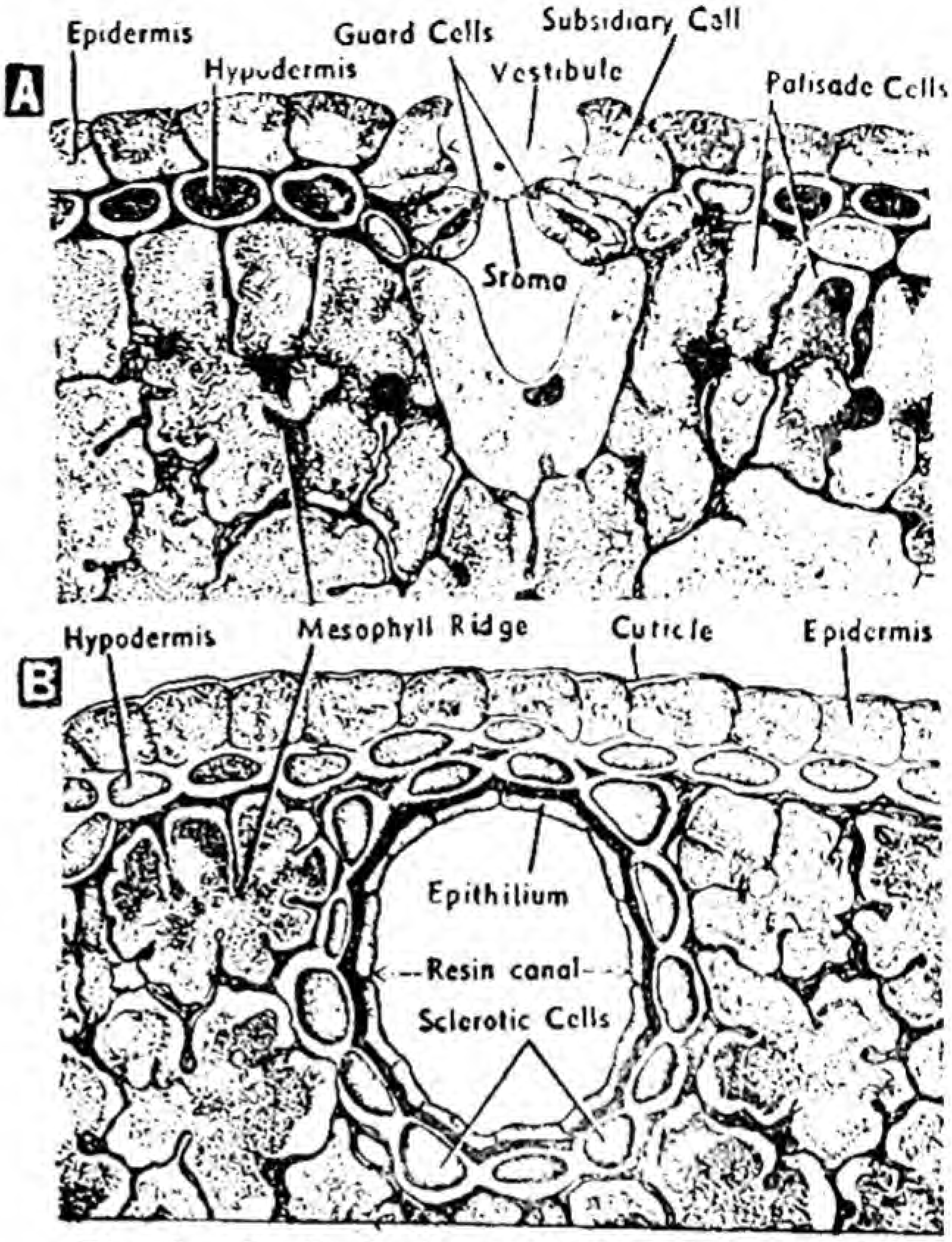


Fig. 7—17 T. S. of a portion of *Pinus* needle A—stomatal apparatus with arm palisade ; B—resin canal with arm palisade (After Esau).

**Microsporophylls (Stamens)**—The microsporophylls or stamens are arranged spirally on a short axis (fig. 7-19). The microsporophylls are scaly and vary from 60 to 135 in number on each strobilus. Each microsporophyll is triangular in outline and consists of a short stalk or filament and leaf-like expanded structure or anther with two pollen sacs or microsporangia borne on the lower or abaxial surface (fig. 7-1). These are filled with microspores or pollen grains. The microsporophylls situated at the base of the strobilus are usually sterile while the upper ones are fertile. The tips of the microsporophylls bend upwards and turn scaly, they thus protect the microsporangia (fig. 7-19).

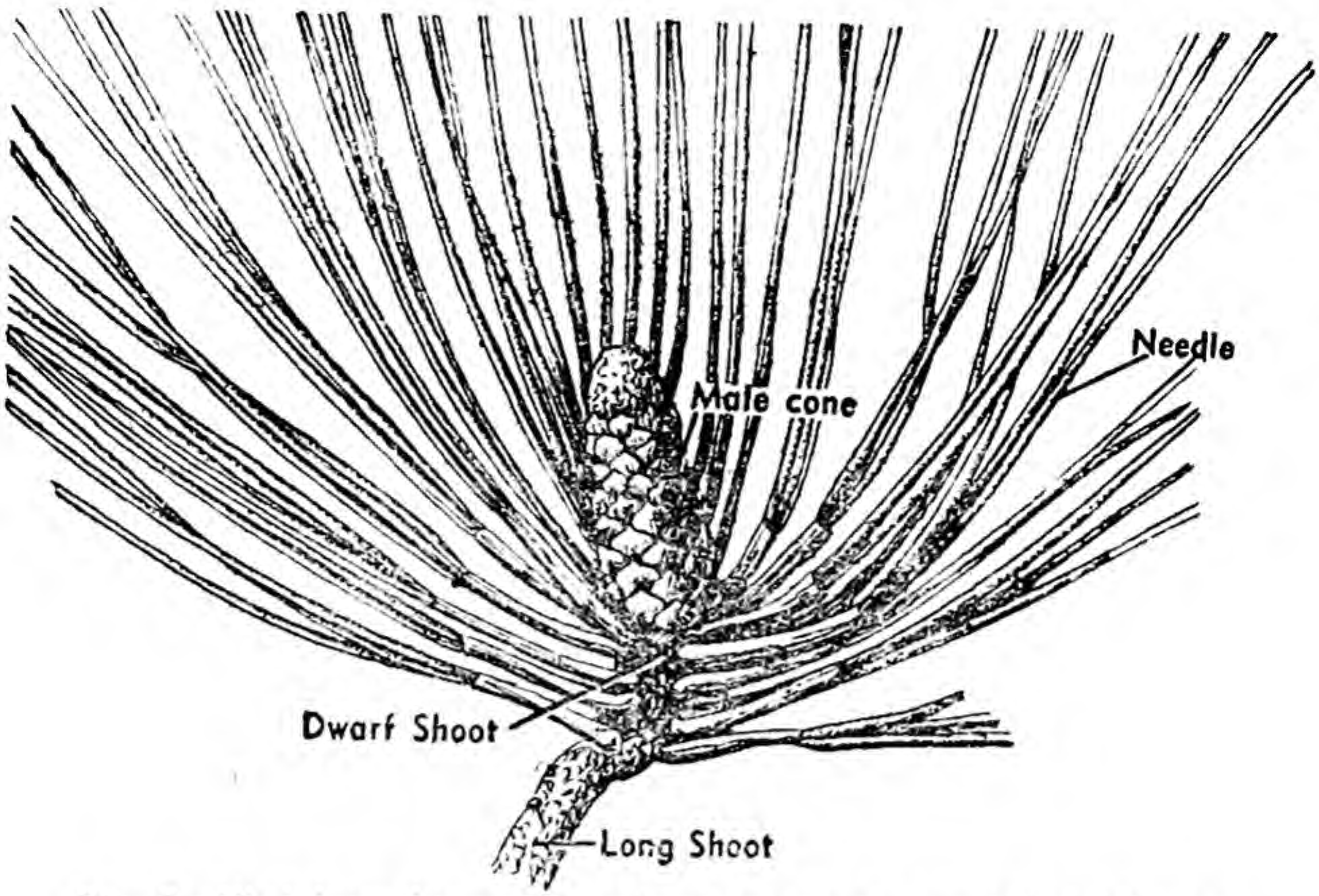



Fig. 7—18 A long shoot of *P. roxburghii* with clusters of dwarf shoots and a male strobilus (After Konar).

**Microsporangia**— Only two microsporangia or pollen sacs are borne on the abaxial or lower surface of each microsporophyll. The development of a microsporangium is of the superficial and eusporangiate type. Allen and Erspamer[1] observed, "In Pinaceae the superficial position of initials of the microsporangium is matched by the active contribution of the surface cells to the formation of the leaf and sporophyll primordia." In several other genera of conifers the primary sporogenous cells are hypodermal. In young stages a microsporangium consists of a few hypodermal archesporial cells which divide to form an outer layer called tapetum and a central mass of archesporial tissue. The

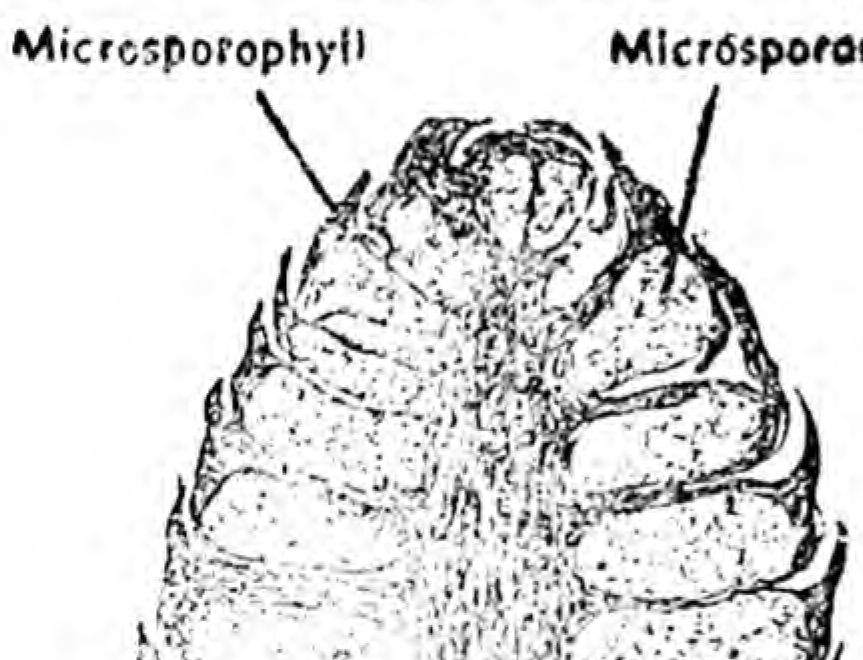



Fig. 7—19 L. S. of the male strobilus of *Pinus sp.* showing microsporangia (After Foster).

1. Allen and Erspamer (Foster, A. S. and E. M. Gifford : 391).

archesporial tissue divides to form a large number of microspore mother cells which represent the last stage of sporophytic generation (fig. 7-20). They divide meiotically or reductionally and each

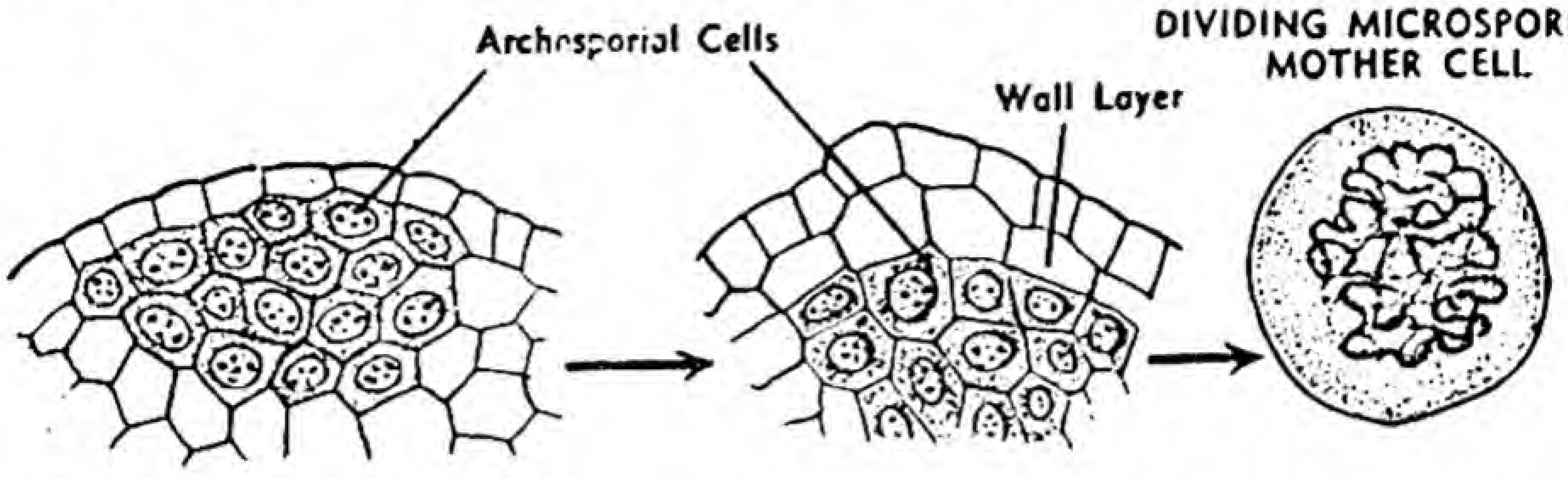



Fig. 7—20 Development of microspore mother cells in *Pinus roxburghii* (After Konar).

microspore mother cell forms four haploid, uninucleate, microspores or pollen grains which latter develop two wings (fig. 7-26 C & D). Konar[1] found that in *P. roxburghii* the microsporangia on matu-

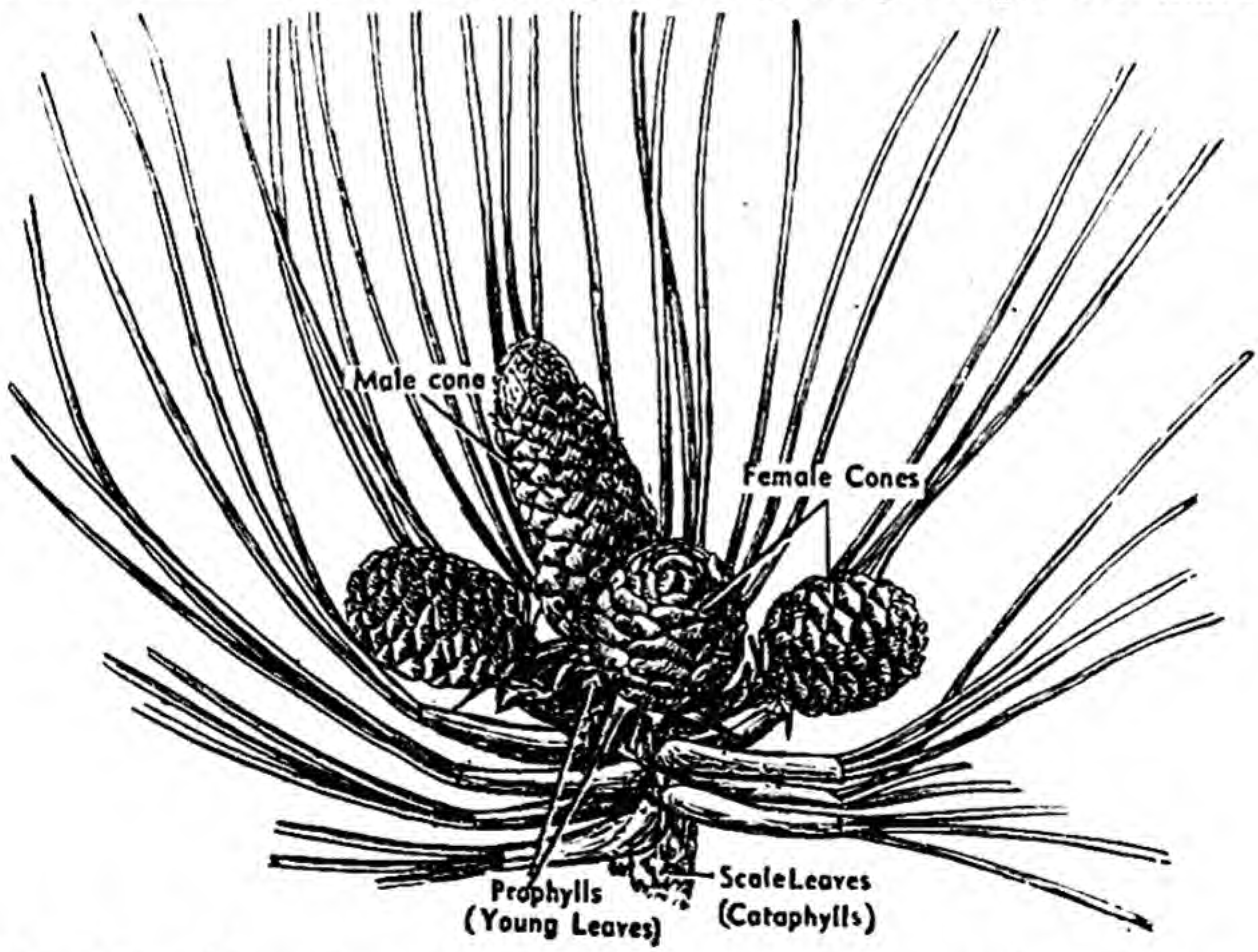



Fig. 7—21 A long shoot of *Pinus roxburghii*, with male and female strobili (=cones), prophylls and cataphylls (After Konar).

rity dehisce through a slit along the long axis. The first shower of pollen grains takes place about the second week of March and

1. Konar, R. N. 1960.

continues for about 15 days. Before the shedding of pollen grains, the male strobilus is about 1 cm long. On maturity its axis elongates considerably and reaches a length of 3 to 4 cm(fig. to 18). The microsporangia, which are now ripe, get separated and discharge their pollen.

**Structure and dehiscence of microsporangium**—Microsporangia are sac-like structures borne on the abaxial surface of micro-

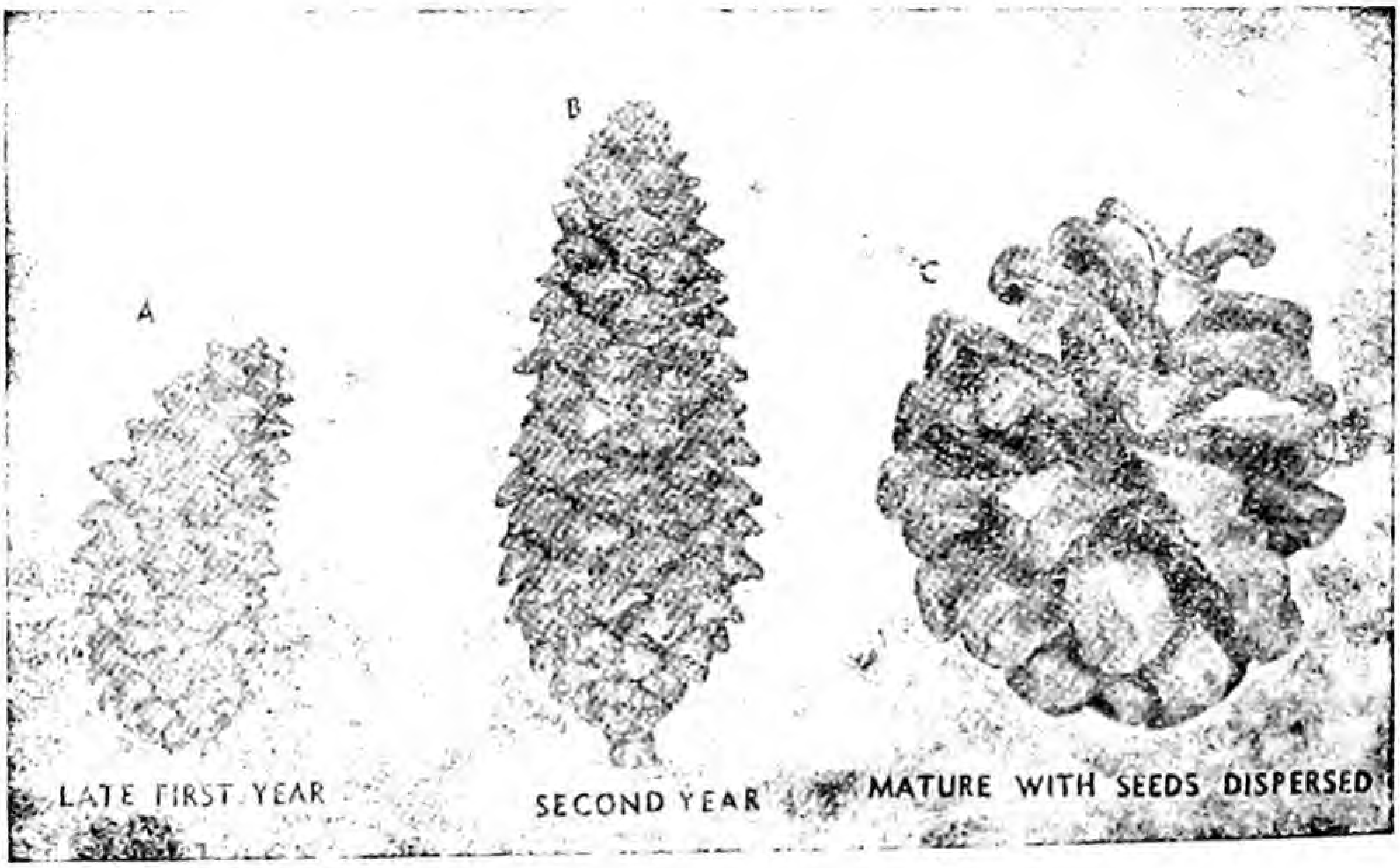



Fig. 7-22 Female strobili of *Pinus roxburghii* A—a young strobilus; B—a mature strobilus at the end of second year ; C—an old strobilus after the shedding of seeds.

sporophylls. They are elongate and sessile and each encloses numerous, light, two-winged microspores or pollen grains (c. f. *Lycopodium* where the sporangia are adaxial and the spores are very small, tetrahedral and unwinged). On maturity the wall of microsporangium bursts from underside revealing a longitudinal slit. A large number of pollen grains get released ; the pale yellow pollen grains cause a cloud which is called 'shower of sulphur'. Pollen grains disperse in the month of March. When the microsporangia become empty, the male strobilus withers and falls off.

**Female strobilus**—The female strobili take three years to completely mature and set seed. They arise in clusters of 1 to 4 in the

axils of scale leaves on shoots of unlimited growth (fig. 7-21) and originate where normally spur shoots would have developed. They are initiated in the month of May in the hills and February in the plains. Konar[1] found that in the plants of *P. roxburghii*, growing in Delhi, female strobili originate in the beginning of March. Prior to pollination bract-scale is larger than ovuliferous

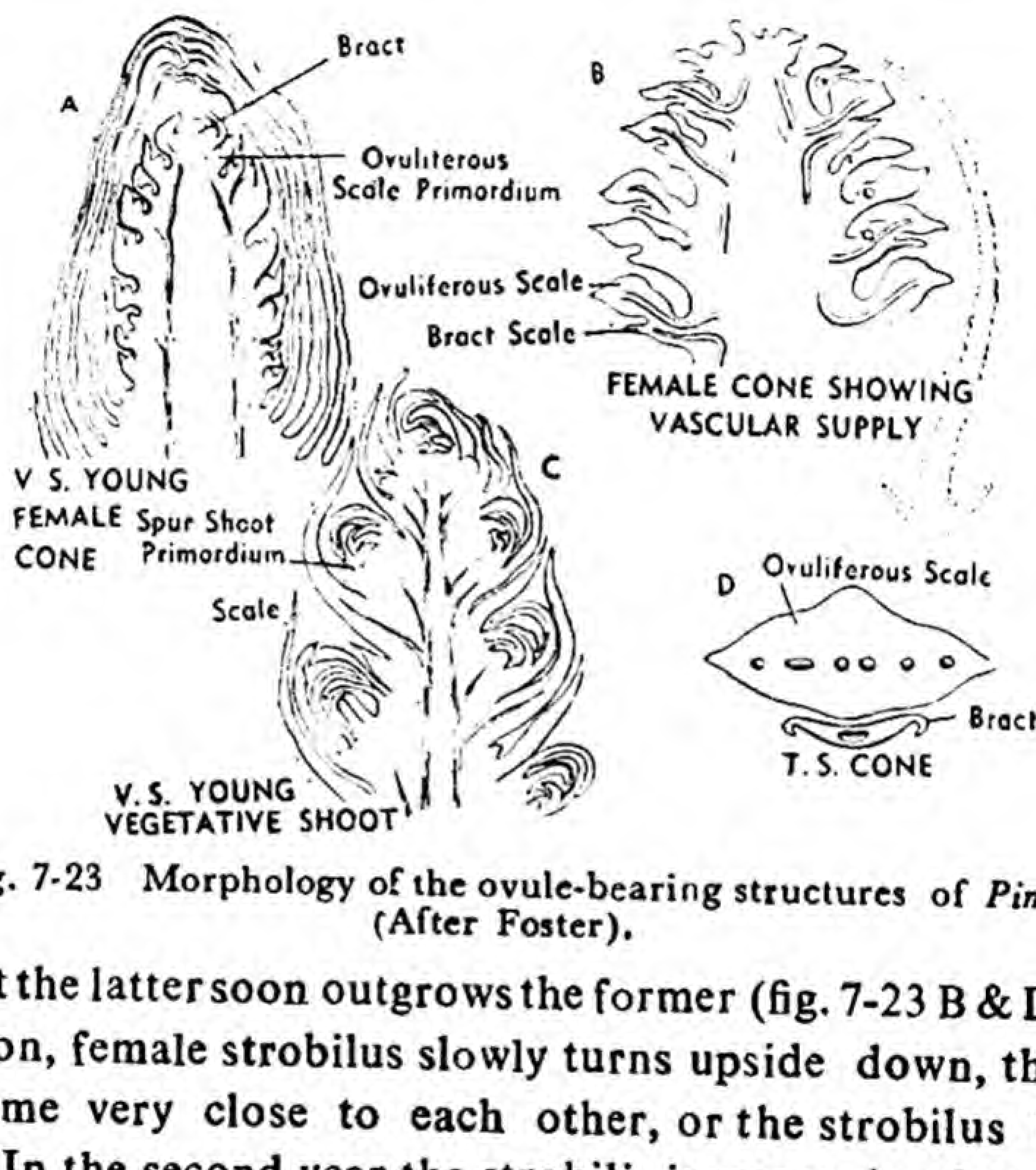



Fig. 7-23 Morphology of the ovule-bearing structures of *Pinus* (After Foster).

scale, but the latter soon outgrows the former (fig. 7-23 B & D). After pollination, female strobilus slowly turns upside down, the sporophylls come very close to each other, or the strobilus becomes closed. In the second year the strobili increase in size until fertilization takes place (fig. 7-22). Female strobili are brown-red in colour, they consist of a central axis on which arise spirally arranged small, paired scales or megasporophylls. The double nature of scales can be easily made out in young stages (fig. 7-23 A,B & D). In adult condition the two are closely appressed. The megasporophyll or the ovuliferous scale, constitutes the upper part and bears ovules It is stout, woody and triangular (fig. 7-25 B). Its terminal broader portion is called the apophysis. The bract, carpellary or cover scale, is situated below the ovuliferous scale.

1. Konar R N. 1960.

It is thin, dry and membranous and has a single vascular strand with the xylem oriented towards the upper surface as in a normal leaf (fig. 7-23 B & D).

**Morphological nature of the ovuliferous scale**—There has been a lingering controversy regarding the morphological nature of the ovuliferous and bract scales of the conifers. Several theories have been advanced from time to time but they were found to be untenable on one ground or the other [1, 2, 3, 4]. Florin's[5] extensive researches conducted to elucidate this vexed problem extend over several years. In order to correctly assess the implications of his work it is essential to study the conifers, which existed during the remote past.

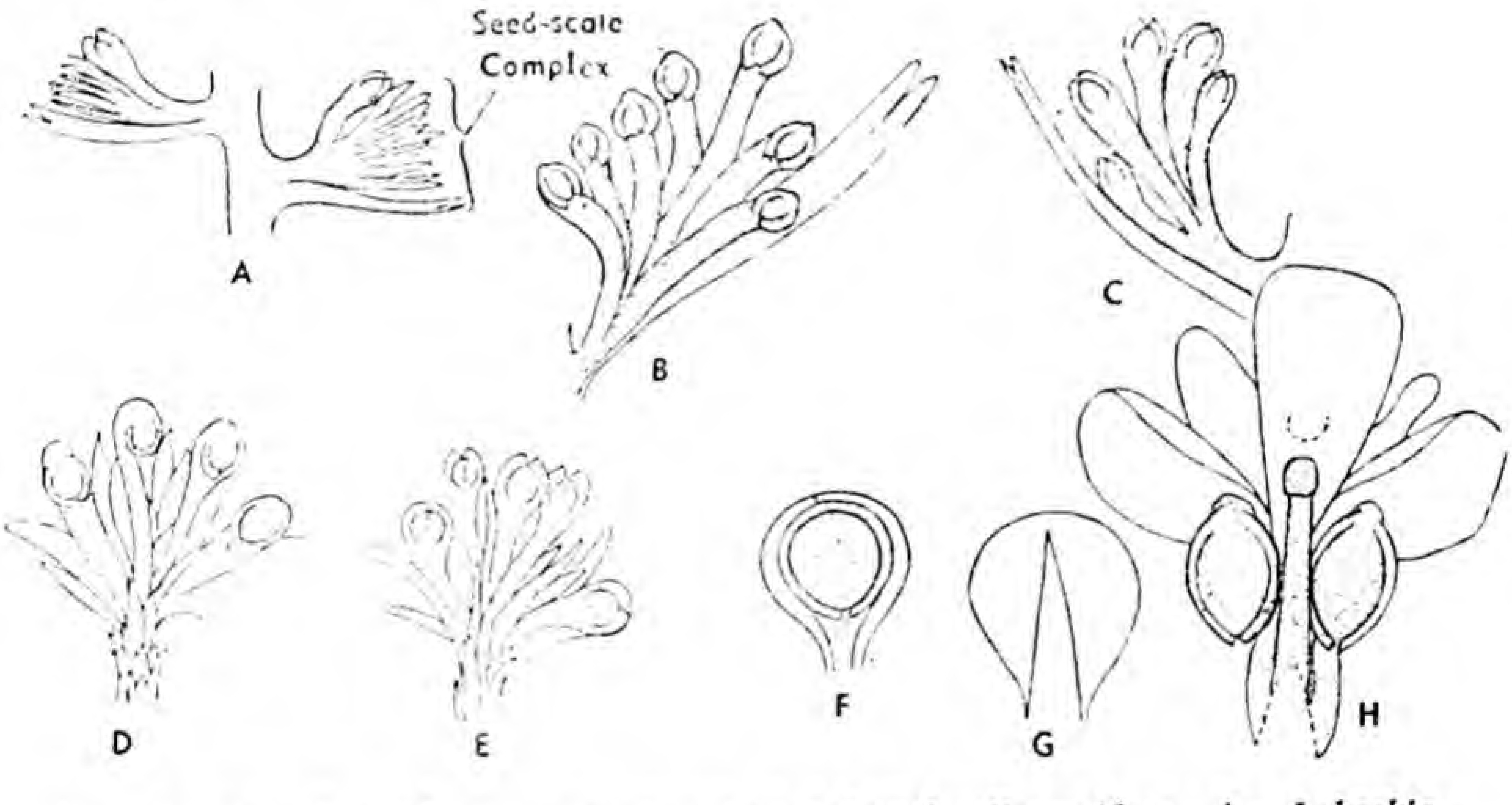



Fig. 7—24 Ovuliferous structures in a few fossil conifers A—*Lebachia goeppertiana*, B—*Walchia (Ernestiodendron ?) germanica*, C—*Ernestiodendron filiciforme*, D—*Walchiostrobus sp.*, E—*Walchiostrobus sp.*, F & G—*Ullmannia bronnii*, (F—upper side, G—underside) ; and H—*Pseudovoltzia libeana* (After Florin).

The Permian genus *Lebachia* had numerous spirally arranged bifid bracts, which in their axils bore small, radial, single ovuled shoots (fig. 7-24 A). All the scaly bracts except one, were sterile; the fertile appendage or megasporophyll situated in the dwarf

1. Sachs, J. 1882.
2. Eichler, A. W. 1889.
3. Kubart, B 1905.
4. Bessey, C. E. 1902.
5. Florin R 1951.

shoot had a single erect ovule. In *Ernestiodendron* the structure was akin to *Lebachia* (Fig. 7-24 B & C) except that the number of fertile appendages was more. The fertile shoots of these fossil conifers are called 'seed-scale complex' by Florin[1], which, according to him, go to show the compound nature of the megasporangiate strobilus ; this being a primary condition in the Coniferales, but not in Taxales. In the upper Permian *Pseudovoltzia* (Fig. 7-24H) the strobilus was composed of spirally arranged entire bracts. Each seed-scale complex was composed of 5 sterile scales and 2 or 3 stalked megasporophylls. Each megasporophyll has a single inverted ovule. Florin[1] believes that fertile shoot of *Pseudovoltzia* corresponds to the ovuliferous scale of recent pine cone with its two inverted ovules. In Triassic genus *Voltzia* the five sterile scales are basally fixed to form a sterile flat structure, the three megasporophylls being adnate for most of their length to the inner surface of these united scales. In *Ullmannia* (Fig. 7-24 F & G) reduction reached an extreme in this that there was a single large flat sterile structure (probably homologous with 5 sterile appendages of *Pseudovoltzia*) and a single fertile appendage with reflexed ovule.

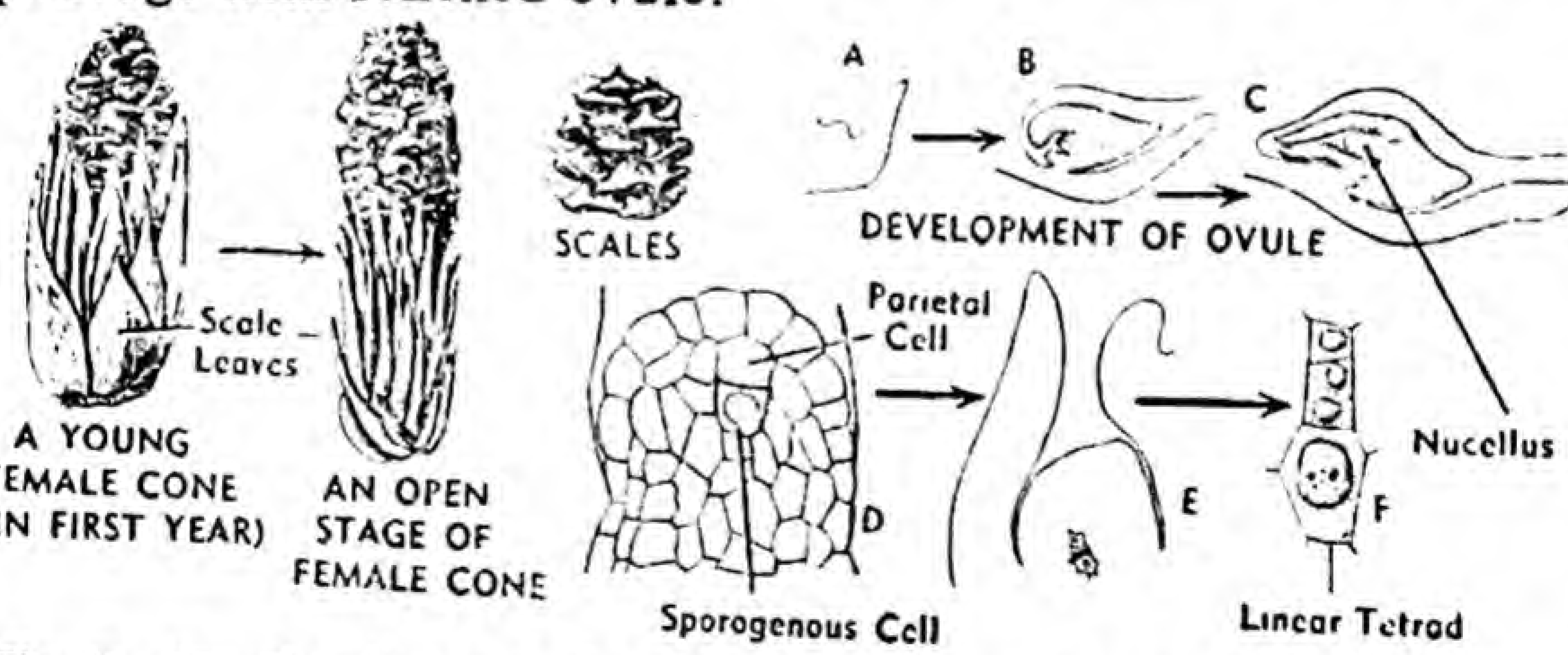



Fig. 7—25 Development of female strobilus and ovule in *Pinus roxburghii* A to C—development of ovule in sectional view ; D to F—formation of megaspores. (After Konar).

**Megasporophylls**—The megasporophylls are arranged spirally on the axis and constitute the female strobilus. Each ovuliferous scale bears two megasporangia or ovules on its upper surface. The micropyles of the megasporangia or ovules are directed towards the base of the scale and the axis of the strobilus.

1. Florin, R. 1951.

**Megasporangia**—Each megasporangium or ovule consists of a central mass of tissue called the nucellus, which is covered over by an envelope. Konar[1] states that in *P. roxburghii* the ovules arise in the third week of February. The nucellus is free from the envelope near the micropylar end only. The envelope at the apex continues into a long tube beyond the nucellus. Micropylar tube or canal is narrow and long. Each ovule arises as a group of cells on the upper or adaxial surface of an ovuliferous scale (fig. 7-25 A to C). At the apex of the nucellus a hypodermal cell enlarges and is then called the archesporial cell. It divides into tapetal and megaspore mother cells. The former forms the tapetum and the latter divides reductionally or meiotically to form four haploid megaspores arranged as a linear tetrad. The three potential megaspores disorganise except the chalazal one which matures into a functional megaspore (fig. 7-25 D to F). It is surrounded by a megaspore membrane, which is ornamented with baculate rods. Pettit[2] considered it to be of the Pinaceae type which differs from the Cupressaceae type as the latter is tigillate.

**Homologies of the reproductive organs** - Certain structures of male and female strobili of *Pinus* are regarded homologous to some structures of heterosporous pteridophytes and angiosperms, these homologies are given below :

| *Selaginella and Isoetes* | *Pinus* | *Angiosperms* |
|---|---|---|
| 1. Microsporangiferous spike | Male strobilus | Naked male flower |
| 2. Axis of the strobilus | Axis of the strobilus | Thalamus of the flower |
| 3. Microsporophyll | Strobilus scale (Microsporophyll) | Stamen |
| 4. Microsporangium | Pollen sac (Microsporangium) | Pollen sac (Microsporangium) |
| 5. Microspore | Pollen grain | Pollen grain |
| 6. Megasporophyll | Megasporophyll proper | Carpel |
| 7. Megasporangium | Ovule (Megasporangium) | Ovule (Megasporangium) |
| 8. Megaspore | Megaspore | Embryo sac |

1. Konar, R. N. 19[illegible]0.
2. Pettit, J. M. 1966.

GAMETOPHYTIC GENERATION—The pollen grains and megaspores have only half the number of chromosomes of a vegetative cell, i. e., they are haploid and hence they represent the beginning of the male and the female gametophytic generations respectively. The basic haploid number of chromosomes in *Pinus* is 12.[1]

**Male gametophyte**—The development of the male gametophyte starts inside the microsporangium long before the shedding of pollen grains (fig. 7-26 A & B). The pollen grains are protected by a cuticularized layer called the exine and an inner thin layer called the intine. The pollen grain divides and cuts off 2 small prothallial cells one after another and a single antheridial cell (fig. 7-26D). The latter divides into a tube cell and a generative cell. The pollen grains are shed at this four-celled stage (fig. 7-26D). The germination of a pollen grain takes place only when it reaches the ovule.

Sterling[2] suggests the following scheme of the development of male gametophyte in *Pinus, Ginkgo* and *Cycas* :

Embryonal cell
↓

| | |
|---|---|
| ↓ First primary prothallial cell | ↓ Embryonal cell ↓ |
| ↓ Second primary prothallial cell | ↓ Antheridial cell ↓ |
| ↓ Generative cell ↓ | ↓ Tube cell |
| ↓ Spermatogenous cell (=Body cell) ↓ | ↓ Sterile cell (=Stalk cell) |
| ↓ Male gamete | ↓ Male gamete |

**Pollination**—In *Pinus*, the pollen grains are carried to the ovule through wind and hence the pollination is anemophilous. Contrary to the popular belief that the wings help in the dispersal of the pollen grains, Wodehouse[3] states that the wings are closed

1. Khoshoo, T. N. 1961.
2. Sterling, C. 1963.
3. Wodehouse, R. P. 1935.

when the pollen grains fly, the wings thus are ineffective in this process. A secretion oozes out through the micropyle during night. It is abundant during night and lasts till morning but later on dries up. It is composed of sucrose, glucose and fructose[1]. The pollen grains get entangled in this fluid. Later,

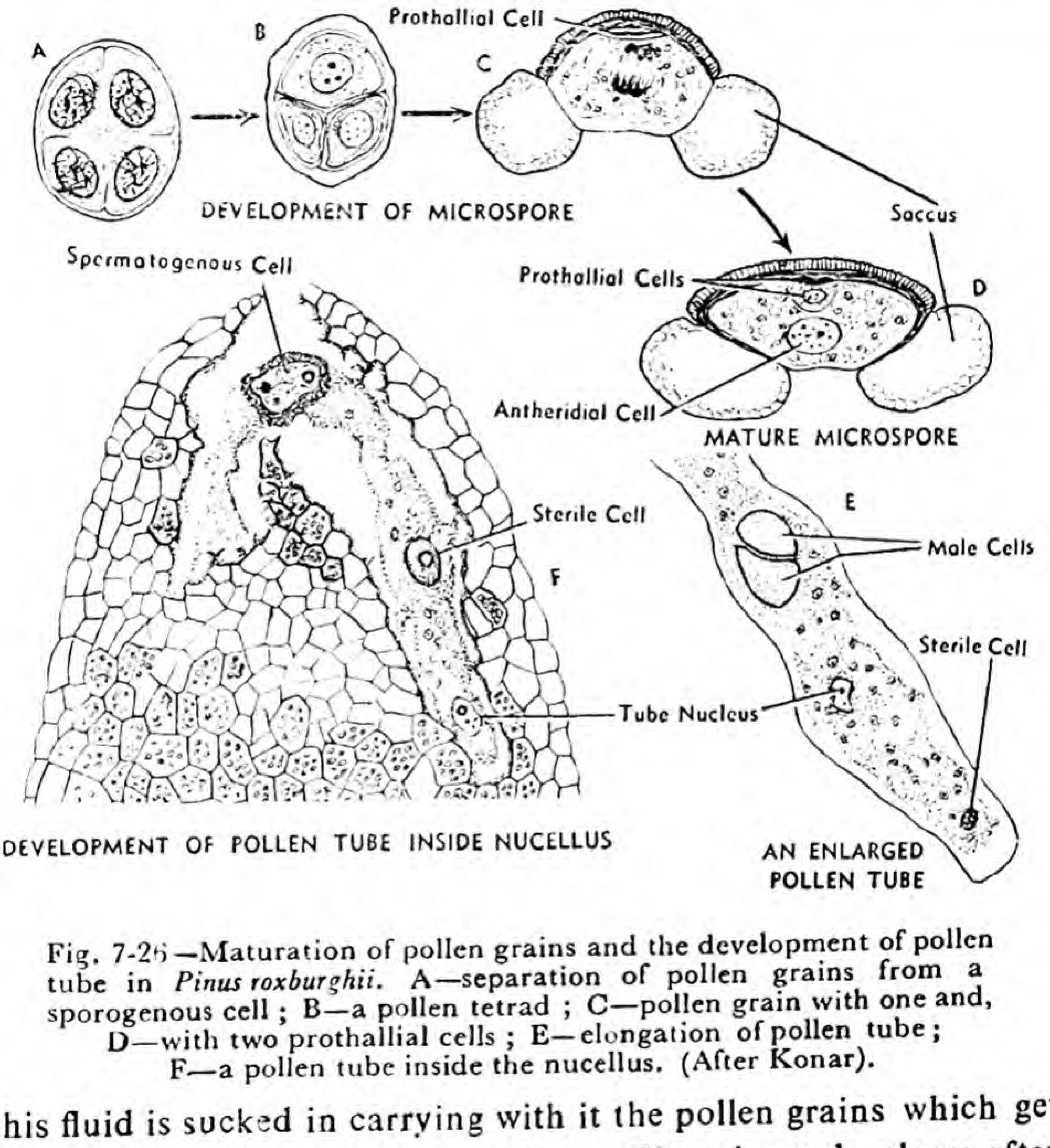



Fig. 7-26—Maturation of pollen grains and the development of pollen tube in *Pinus roxburghii*. A—separation of pollen grains from a sporogenous cell ; B—a pollen tetrad ; C—pollen grain with one and, D—with two prothallial cells ; E—elongation of pollen tube ; F—a pollen tube inside the nucellus. (After Konar).

this fluid is sucked in carrying with it the pollen grains which get deposited at the apex of the nucellus. The micropyle closes after pollination. It is known that in some species of *Pinus* this closure is forceful and trapped grains get crushed by it[2]. Pollination occurs in the months of May-June in the hills and February-March in the plains.

1. Dogra, P. D. 1964.
2. McWilliam, J. R 1958.

**Female gametophyte**—The female strobilus increases in size slightly in the first summer following pollination and more rapidly during the next year when fertilization is to take place. Megasporophylls turn hard and brown on maturity. Now the two kinds of scales become almost indistinguishable.

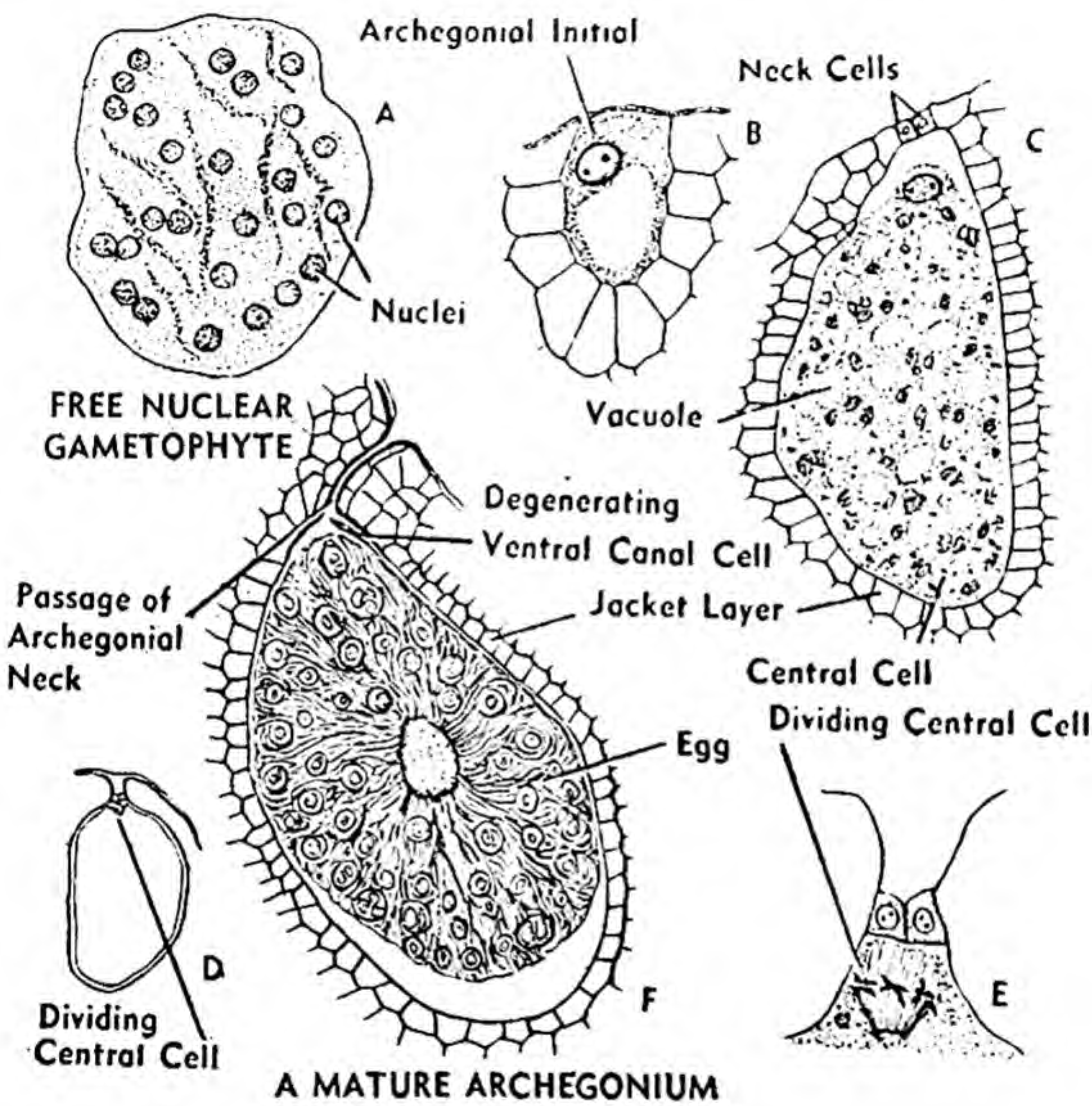



Fig. 7—27. Stages in the development of female gametophyte of *Pinus roxburghii* A—free nuclear stage of the gametophyte; B—an archegonial initial; C—a young archegonium with 2 neck cells and a central cell; D & E—stages of the division of central cell; F—a mature archegonium with degenerating ventral canal cell (After Konar).

The functional megaspore enlarges in size. A vacuole appears in its centre and the megaspore nucleus divides by free-nuclear divisions (fig. 7-27A). Thus nearly 2,000 small nuclei[1] are formed without walls. Each nucleus later gets

1. Ferguson, M. C. 1904.

invested by a wall. The formation of these walls starts from the periphery in a centripetal fashion. The massive tissue so formed is called 'the endosperm' or 'female prothallus'. Corresponding to the tapetum, a two-layered nutritive or spongy tissue is also formed round the endosperm by the tissue of the nucellus. Now, two or three superficial cells of the female gametophyte at the micropylar end become slightly enlarged and prominent. These are the archegonial initials (fig. 7-27 B). Each initial divides to form a primary neck cell and a large central cell (fig. 7-27 C). The primary neck cell undergoes three divisions and forms eight neck cells which are arranged in two tiers* of four cells each. The central cell divides to form a ventral canal cell which is separated from a large egg by a definite wall [c f. *Cycas* where no such wall exists] (fig. 7-27 Dto F). Venter of the archegonium remains embedded in the tissue of the female gametophyte. Neck canal cells are absent.

**Fertilization**—After an year of pollination, fertilization takes place. Konar[1] states that fertilization in *Pinus roxburghii* occurs at the end of April or in the beginning of May. The microspores or pollen grains resting on the nucellus germinate directly (as there is no pollen chamber). The generative cell now divides into two, a sterile or stalk cell and a spermatogenous or body cell (fig. 7-26 E & F). The pollen germinates and forms a pollen tube distally. The spermatogenous or body cell divides and forms two male cells or gametes (fig. 7-26 E) which are nonflagellate but one of them may be slightly larger than the other. These show amoeboid movement. By this time the pollen tube, which is said to be non-haustorial, pierces the nucellus and reaches the neck of the archegonium (fig. 7-26 F). On coming in contact with the archegonial neck the pollen tube bursts at the apex of the archegonium and both the male cells or gametes are liberated. Only one of the male cells, however, fuses with the egg nucleus and forms the zygote (fig. 7-28 A to C), the other male gamete disintegrates along with the sterile or stalk and tube cells. Fertilization usually occurs towards the end of June. The zygote, being

*Tier is pronounced as tear.

1. Konar, R. N. 1960.

diploid, possessing 24 chromosomes, represents the beginning of the sporophytic generation.

DEVELOPMENT OF EMBRYO—The zygote, as a result of three divisions, forms an eight-celled structure, the primary proembryo (fig. 7-28 D to H). It consists of two primary tiers[1] of

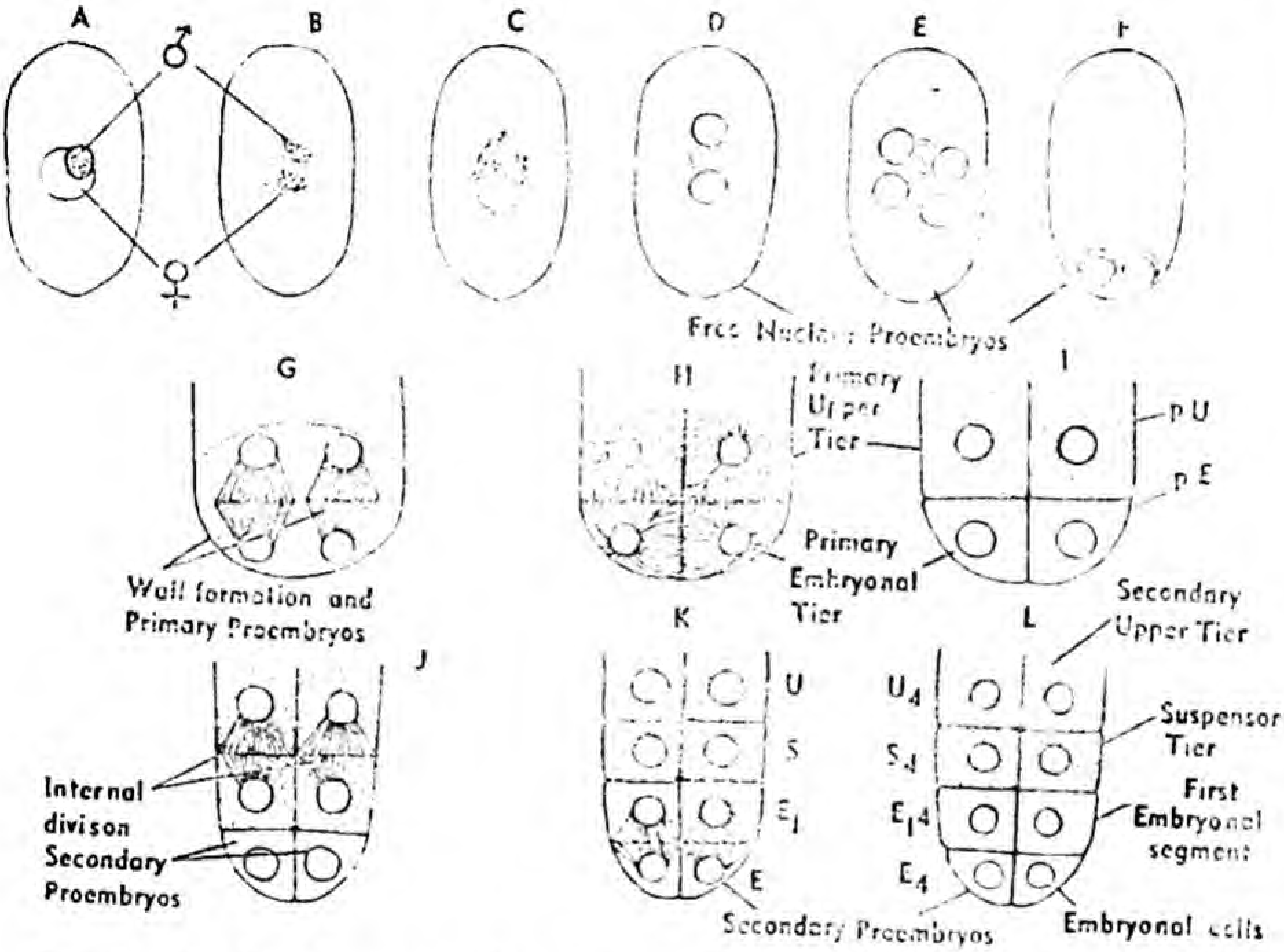



Fig. 7—28 Development of proembryo from fertilization to the formation of secondary proembryo in Pinaceae. A to C—fusion of male and female nuclei, D to E—free nuclear divisions, F—last free nuclear stages, G & H—wall-formation, I—formation of primary upper and primary embryonal tiers, J—internal division of primary upper tier, K & L—formation of four different tiers. The numbers after the letters e. g., $U_4$, $S_4$ etc., indicate the number of cells that constitute the tier (After Dogra).

four cells each. The upper or open tier has been termed, the primary upper tier or pU (fig. 7-28I) and the lower or apical, the primary embryonal cells[3] or pE (fig. 7-28I). The internal division[2] (fig 7-28 J & K), taking place in the cells of the primary

1. Tier is a term applied to the embryonal cells lying in horizontal plane.
2. Boyle P. & J. Doyle 1954
3. Dogra, P. D. 1967

proembryo, results in the formation of the secondary proembryo (fig. 7-28 J to L). The different regions of the secondary proembryo have now been designated as under[1] :

Open tier → Secondary upper tier (U) (figs. 7-28 K & L, 7-29A)

Rosette tier → Suspensor tier (S) (figs. 7-28 K & L, 7-29A to C)

Suspensor tier → First embryonal segment ($E_1$) (figs. 7-28L, 7-29 A to D)

Apical tier → Embryonal cells (E) (fig. 7-28 L)

It has been observed that the primary upper tier forms the secondary upper (U) and suspensor tiers (S), while the primary embryonal cells develop the first embryonal segment ($E_1$) and the embryonal cells (E) (fig 7-28 I to L). Each of these four tiers usually consists of four cells (fig. 7-28 L). Secondary upper (U) and suspensor (S) tiers, having no function in Pinaceae, degenerate (figs. 7-28 K & L, 7-29 A to D). Suspensor tier (S) sometimes divides irregularly and the irregular proliferations, so formed, were previously termed rosette embryos. Because these rosette tiers have not been observed to develop in Pinaceae, the term rosette embryo has been discarded.

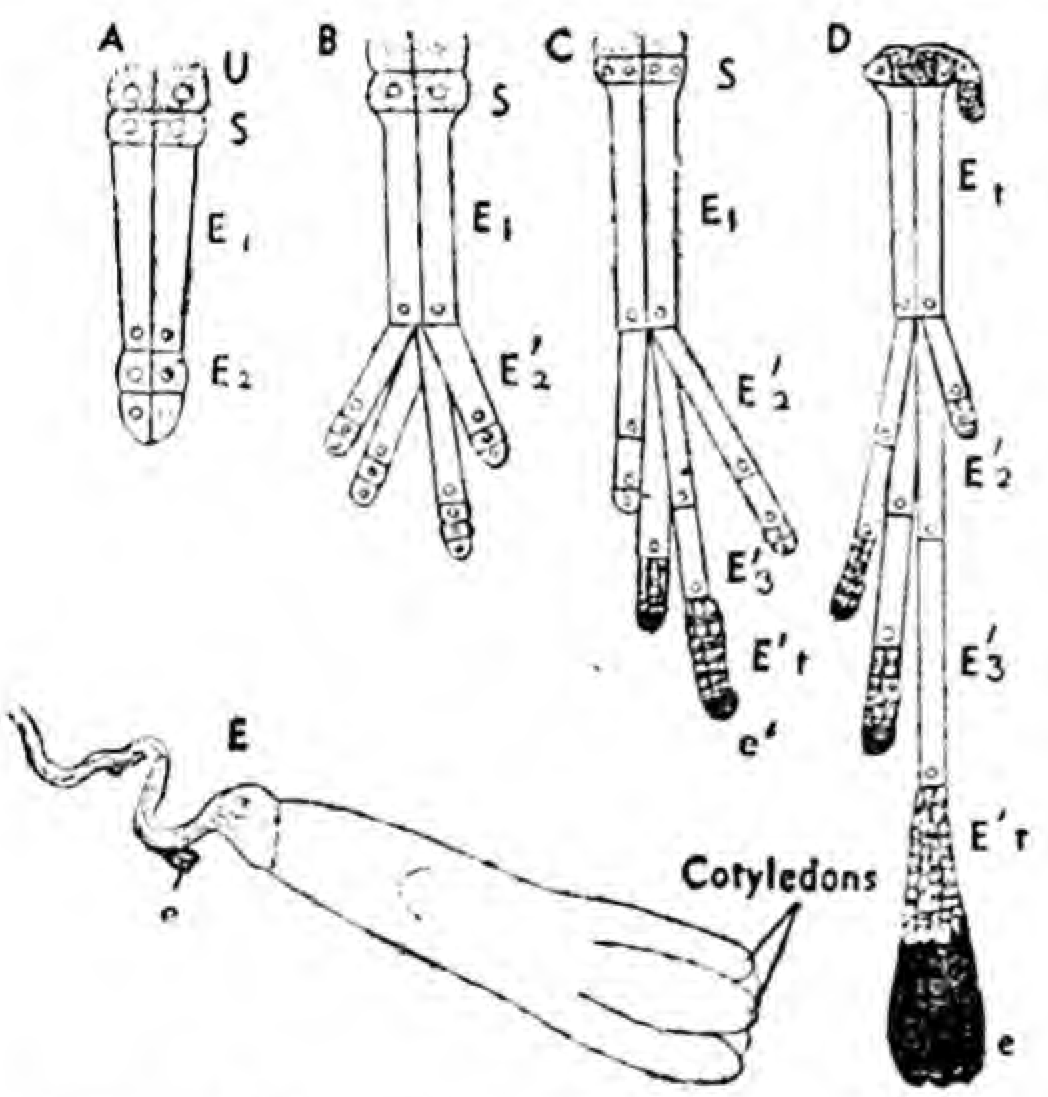



Fig. 7-29 Late embryogeny of Pinaceae. A—elongation of first embryonal segment ( $E_1$ ), B to D—elongation of further segments of first embryonal segment ($E'_2$ , $E'_3$ ,Et) and the formation of embryonal mass of cells (e), E—an embryo with cotyledons (After Dogra).

1. Doyle. P. 1957, 1963.

During the later development of embryo, the prothallial tissue, in the form of a conical region, called corrosion region, gets differentiated below the archegonia (fig 7-30). The cells of corrosion region serveas a nutritive tissue during the development of embryos. The outer region of the female gametophyte, composed of the storage tissue (fig.7-30) or gametophyte is used up during the germination of the seed. The proembryonal stage, in Pinaceae, ends with the elongation of first embryonal segment (fig. 7-29 A to E).

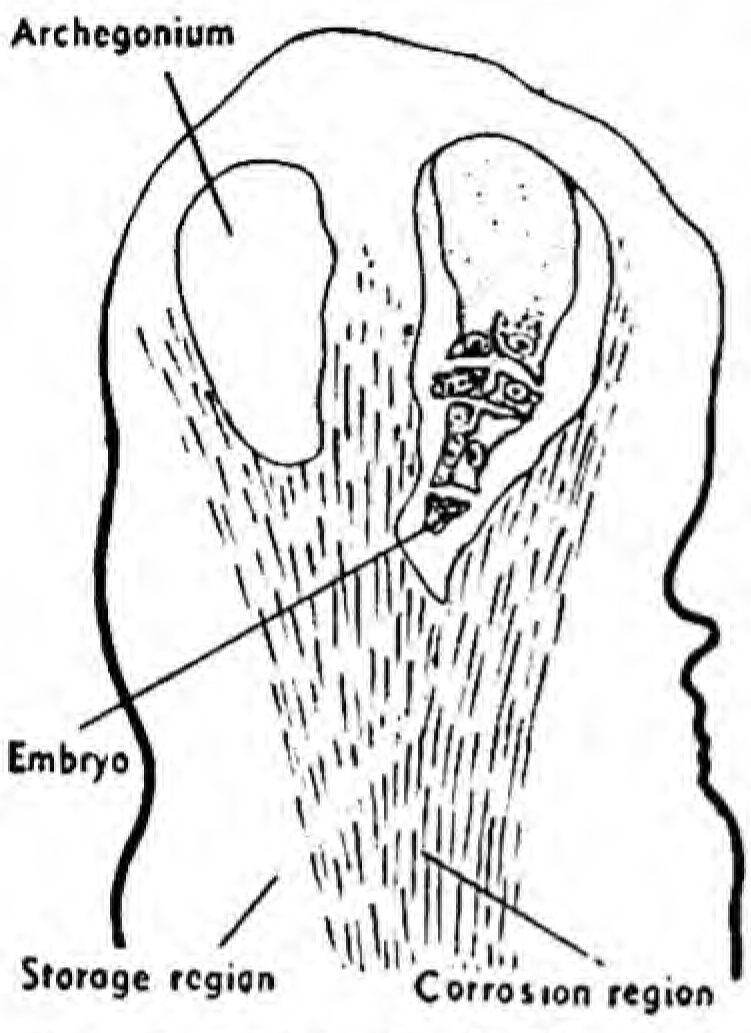


Fig. 7 — 30 Prothallus of *Picea smithiana* with an archegonium, embryo and corrosion region (After Dogra).

Thus in *Pinus* a single zygote may form several embryos after the splitting up of the developing proembryo, this phenomenon is called 'cleavage polyembryony'. Usually a single zygote forms four embryos but only one of them matures. In case 2 or 3 archegonia are fertilized the number of embryos formed is a multiple of 4 (i. e. 8, 12 or even more embryos may develop). Ultimately, however, only one embryo develops inside a seed, others perish. In the centre of the seed which is full of endosperm lies a straight axis, consisting of the radicle pointing towards the micropyle and the plumule opposite it. The latter is included within the cotyledons. The number of cotyledons (fig. 7-29 E) is always more than two and varies from 8 to 14 and they are green whilst enclosed within the seed[1].

Konar[2] has studied the life-history of *P. roxburghii*. He observed that various stages of micro- and megasporogenesis, gametophytic development and the embryogeny take place in different months of the year. These are shown in a tabular form

1. Willis, J. C. 1966
2. Konar, R. N. 1960.

below:

| Month | Male | Female |
|---|---|---|
| | **CHANGES OCCURRING IN THE FIRST YEAR** | |
| Jan. | Period of slow growth of strobilus | Initiation of female strobilus. |
| Feb. | Formation of binucleate tapetum. Degeneration of wall layers. Development of fibrous thickenings, formation of uninucleate pollen grains and beginning of the development of male gametophyte. | Differentiation of hypodermal archesporial cell. Emergence of female strobilus out of cover scales. |
| March | Development of two prothallial cells, a tube cell and a generative cell, shedding of pollen grains. | Pollination. Closure of micropyle. Free nuclear divisions in megaspore to form 18 to 32 nuclei. |
| April | Germination of pollen grains on nucellus. | ........... |
| May Aug. | Rest period. | Rest period. |
| Sept. | Initiation of fresh crop of male strobili. Formation of archesporial cells. | .... .. .. |
| Oct. | Growth of microsporangia. Formation of wall layers. | ..... ...... |
| Nov. | Differentiation of tapetum. | ...... ...... |
| Dec. | Period of slow growth. | ............. |
| | **CHANGES OCCURRING IN THE SECOND YEAR** | |
| Jan. | Rest period. | Rest period. |
| Feb. | ............. | Renewed growth of female strobilus Resumption of free nuclear divisions. Gradual increase in the size of strobilus. Further division and enlargement of free nuclear gametophyte. |
| March | Division of generative cell to form a stalk cell and a body cell. Migration of stalk cell and body cell Division of body cell to form two male gametes. | Basal subtending scales of female strobilus drop off. Wall formation in gametophyte and further divisions resulting in the increase of cells. Initiation and enlargement of archegonial initials. |

| Month | Male | Female |
|---|---|---|
| April | Growth in the size of one male nucleus, the other is slightly smaller. Fertilization. | Divisions resulting in the formation of primary neck cell. Formation of 4 neck cells. Growth of central cell. Formation of ventral canal cell and egg cell. Enlargement of egg nucleus. Fertilization. Division of zygote to form 4 nuclei. Formation of the suspensor and embryonal tiers. |
| May | .......... | Growth of proembryo |
| June | .......... | Growth and differentiation of embryo. |
| July-Dec | ...... .... | Maturation of embryo. |
| | CHANGES OCCURRING IN THE THIRD YEAR | |
| Jan-March | .......... | Maturation of embryo |
| April | .......... | Opening of strobilus and shedding of seeds. |

**Structure of seed**— After the formation of embryo the ovule is called a seed. A fully mature seed (fig. 7-31 A to E) has the following structures:

(i) Embryo—It develops from a part of the zygote and consists of root, stem-tip and 8 to 14, cotyledons (fig. 7-31 A & B). It represents the newly formed sporophytic generation.

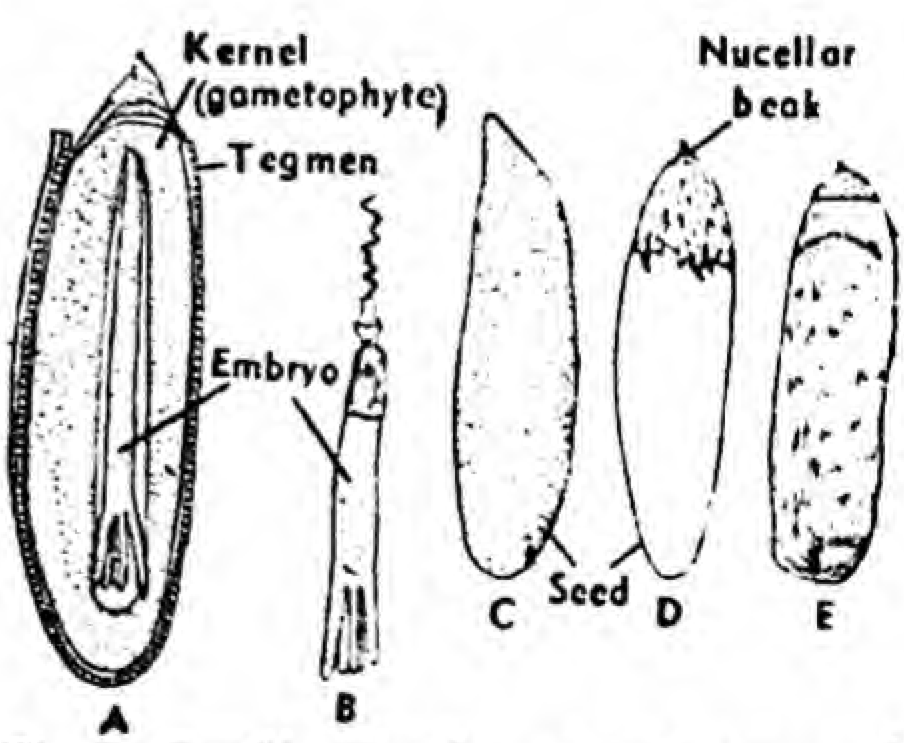



Fig. 7—31 Seed structure of *Pinus gerardiana*, A—V.S. of the seed, B—a mature embryo, C—a complete seed, D—kernel with nucellar cap, without seed coat and E—a seed, with outer seed coat removed (After Dogra).

(ii) Gametophyte or Kernel—It is a nutritive tissue composed of cells possessing haploid number of chromosomes (fig 7-31A). This tissue surrounds the embryo. It is white in colour and oily in nature.

(iii) Perisperm—It is a thin, membranous, reddish brown and papery structure which helps in serving as a nutritive tissue to the developing embryo. It is a remnant of the nucellar tissue, and, hence possesses diploid number of chromosomes.

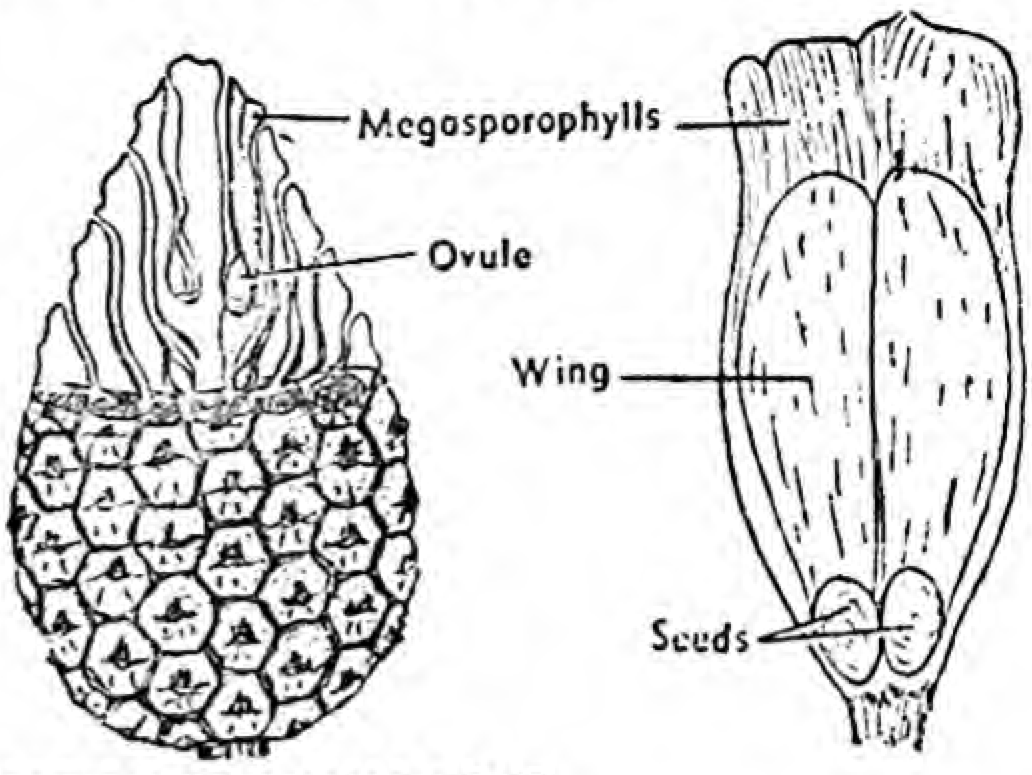


Fig. 7—32 Portion of a female strobilus of *Pinus* and a single megasporophyll with 2 winged seeds (After Coulter and Dittmer).

(iv) Seed coat—It develops from the middle stony layer of the envelope and is the outermost covering of the seed (The outer fleshy layer of the envelope disappears). The innermost layer of envelope is sometimes present as a thin membrane.

(v) Wing—It is a membranous structure formed from the thin layer of tissue which splits from the adaxial (upper) surface of the ovuliferous scale (fig. 7-32). It helps in the dispersal of the seed by wind to long distances.

**Germination of seed**—With the maturation of the seeds the axis of the strobilus, as a result of its renewed growth, elongates. It sometimes emits a crackling sound. The elongation of axis results in gaping apart of the scales, the seeds, when shaken out from strobilus by wind, escape (fig. 7-22C). Under favourable conditions the seeds may germinate without undergoing a period of rest. Under unfavourable circumstances these may remain dormant for several months or years. If suitable conditions are available the seed coat splits and the radicle grows into the soil drawing nourishment from the endosperm. The plumule grows above the soil and carries the cotyledons which are already green. Germination is thus epigeal (fig. 7-33). The cotyledons are said to be green even while inside the seed coat[1]. Konar[2]

1. Willis, J. C. 1966.
2. Konar, R. N. 1960.

reports that in *Pinus roxburghii* 8 to 14 cotyledonary leaves are formed, these develop on the shoot of unlimited growth. They are 2 to 6 cm long, acicular, trigonal in cross section and pale-green and consist of sheathing leaf-bases (fig. 7-33). The radicle develops and forms the primary tap root, the plumule forms the shoot of unlimited growth on which arise simple acicular leaves. These juvenile leaves unlike the adult ones are simple. As the plant grows and becomes mature they become smaller till they become reduced to small papery, brown structures called the scale leaves. In their axils arise the dwarf (=spur) shoots which bear the adult leaves( = needles). The juvenile leaves are spirally arranged on long shoot. The growth of pine plant is slow.

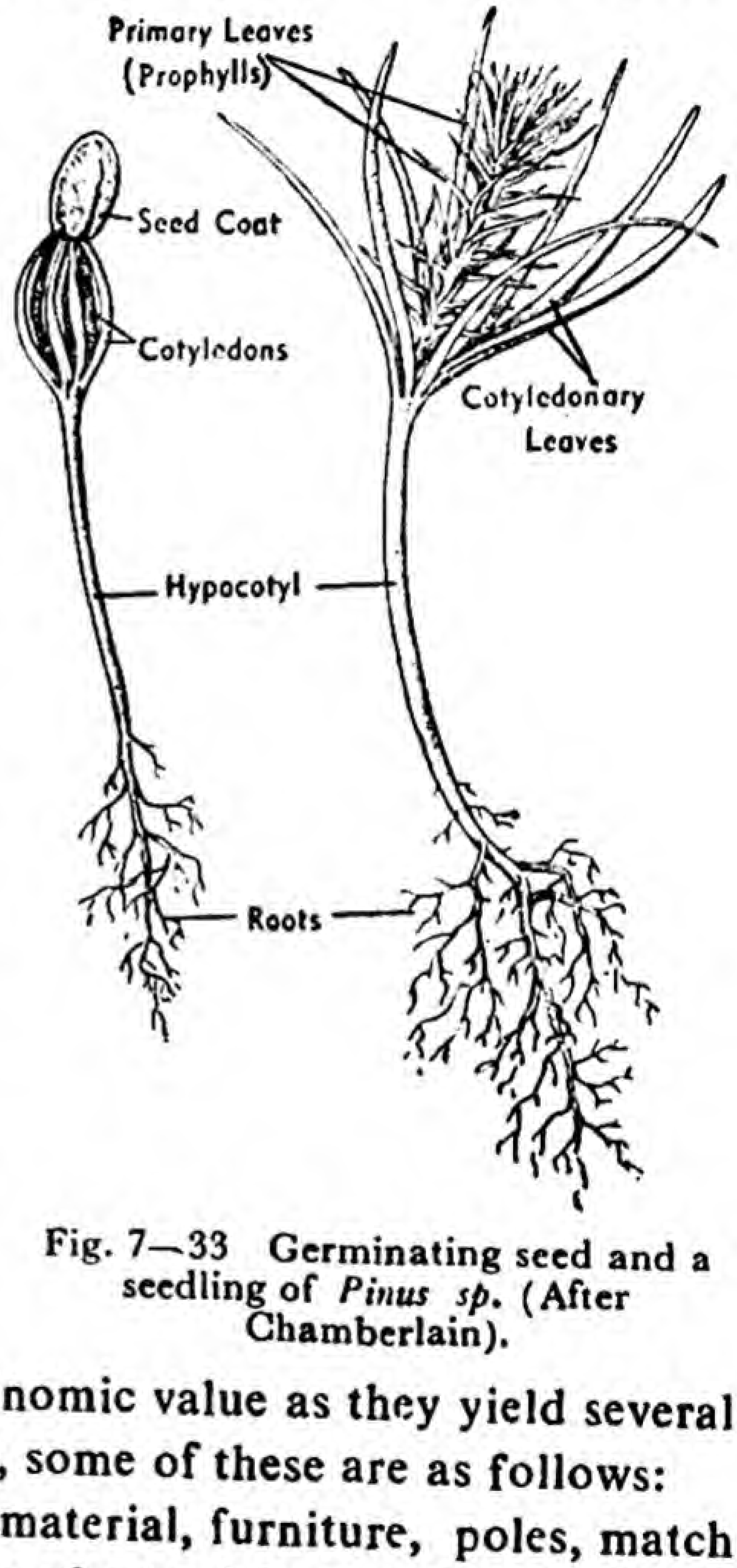


Fig. 7—33 Germinating seed and a seedling of *Pinus sp.* (After Chamberlain).

ECONOMIC IMPORTANCE—The different genera of Coniferales are of great economic value as they yield several commercial products of daily use, some of these are as follows:

**Timber**—Wood for building material, furniture, poles, match boxes and other articles are obtained from different species of *Pinus, Cedrus* and *Abies*. **Paper**—Paper pulp is mainly obtained by crushing the wood of *Picea* into fine bits and then bleaching it. **Pencils**—Wood for making pencils, scales and holders, etc., is obtained from *Juniperus virginiana* Linn. **Organic chemicals**—Turpentine, resin, canada balsam, tannins, varnishes and several other useful products are obtained by the distillation of the wood of several

species of *Pinus Abies, Larix* etc. **Food value**—Seeds of *Pinus gerardiana* are edible and are sold in the market under the name of 'chilgoza'. The seeds of *P. roxburghii* are also eaten by hill people. In all 5 species of pines produce edible seeds

Many different Indian species of *Pinus* are of economic value. *P. gerardiana* yields edible seeds the 'chilgoza'; *P. roxburghii* and *P. wallichiana* are important sources of timber which is used for furniture-making and various other purposes. Different species of *Pinus* provide a cheap source of cellulose and are planted for their beautiful appearance. *P. insularis* and *P. roxburghii* are the chief sources of resin and turpentine.

## OTHER GENERA OF PINACEAE

*Cedrus* Trew.— *Cedrus deodara* Loud. (Deodar) is a tall evergreen tree possessing horizontal pendulous branches. Leaves are needle-like, nearly 2 50 cm long. Plants are monoecious or dioecious, male strobili are numerous and erect; these arise singly at the end of leaf-bearing branches Stamens are spirally arranged, each with two adjacent pollen sacs. Female strobilus at maturity is erect, barrel-shaped, ovoid and brown in colour (fig. 7·34) Megasporophylls are spirally arranged, fan-shaped, closely overlapping, deciduous, each has two ovules at the base which later become seeds. The megasporophylls are thin at the apex and thick at the base. Seeds are nearly 0 64 cm long. Cotyledons are 9 to 10. Strobili mature after two years of pollination, and break up while on branches. *Cedrus* grows at an altitude of 1800 to 2550 metres above sea level. It grows in abundance in the Western Himalayas

*Picea* Dietr.— *Picea smithiana* Boiss and *P spinulosa* Beissn. are the two commonly occurring species of *Picea* (spruce) in India. The trees are tall with horizontal branches and conspicuously

drooping branchlets. Leaves are bluish or greyish-green, nearly 2.5 cm long, needle-like incurved, four sided. Plants are monoecious. Male strobilus is about 2.5 cm long and erect. Female strobilus is solitary and terminal in position, pendulous when mature. Seeds are small, nearly 0.42 cm in length. Wing is spatulate. The wood is used as an important timber and the wood pulp is used in manufacturing paper. In India the trees grow between an altitude of 2100 to 3300 metres in the Western Himalayas.

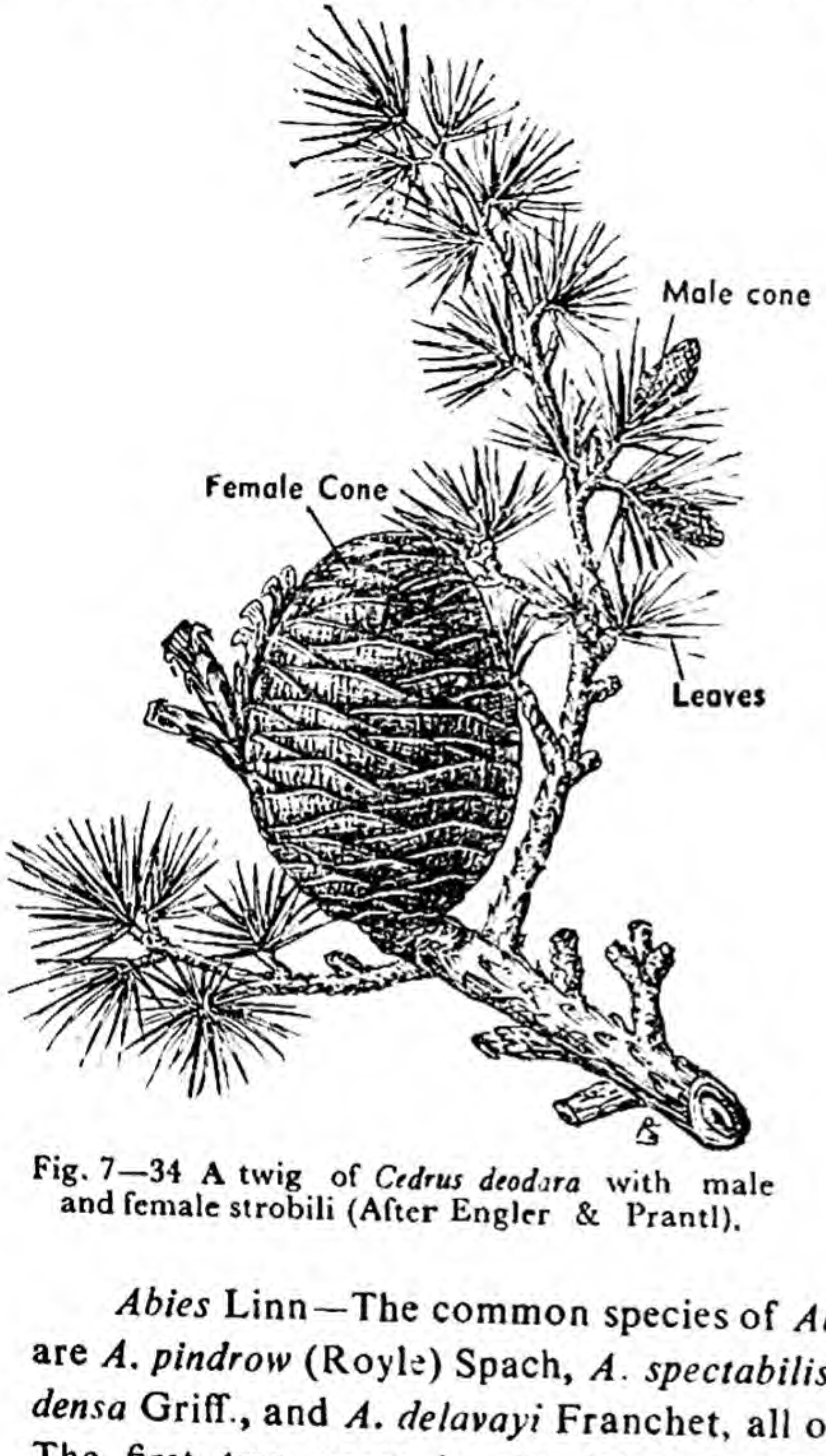


Fig. 7—34 A twig of *Cedrus deodara* with male and female strobili (After Engler & Prantl).

*Abies* Linn—The common species of *Abies* that grow in India are *A. pindrow* (Royle) Spach, *A. spectabilis* (D. Don) Spach. *A. densa* Griff., and *A. delavayi* Franchet, all of which are tall trees. The first two grow in the Western and the latter two in the Eastern Himalayas within the altitudinal range of 2100 to 4500 metres. In Western Himalayas *A. spectabilis* occurs at higher elevation than *A. pindrow*. Leaves are flattened, linear, notched at the apex and spirally arranged. The upper surface of the leaves is dark-green while the lower is shining and silver-white. Plants are monoecious, male strobili are sessile and clustered. Female strobilus is erect, terminal and solitary. Bracts are ovoid and resistant. Wing is round and seeds are nearly 0.84 cm long.

The cones break up as soon as the seeds are ripe, leaving the persistent cone-axis on the tree. The plants grow gregariously in the Western Himalayas between an altitude of 1200 to 3500 metres. *Abies pindrow* is planted near temples. Railway sleepers are made from its wood.

*Tsuga* Carr.—The only species that occurs in India is *T. dumosa* (D. Don) Eichler. It is an evergreen tree with drooping branches and linear leaves possessing knee-shaped stalk, seated on tuberculate cushion. Upper surface of the leaf is dark-green and the lower silvery-white. There occurs a resin canal below the midrib of the leaf. Young shoots are light brown. Plants are monoecious. Strobili are axillary or terminal, small, round and pendulous. It grows between an altitude of 2400 to 3000 metres from Kumaon to Bhutan in the Eastern Himalayas.

Chapter 8

# Taxales

This group was formerly embraced by the family Taxaceae[1, 3] which included besides the present genera of the Taxales, members of the Podocarpaceae and Cephalotaxaceae. The order Taxales, with a status equivalent to Coniferales, now includes, according to Florin[2], five genera, namely *Taxus* Linn, *Austrotaxus* Compton, *Pseudotaxus* Cheng. (=*Nothotaxus* Florin), *Amentotaxus* Pilger and *Torreya* Arnott. All these constitute a single family Taxaceae. These genera, according to Hui-Lin Li[4] and Turrill[5], have a total of 19 species viz., *Amentotaxus* (4 spp.), *Torreya* (6 spp.), *Austrotaxus* (1 sp.), *Nothotaxus* (1 sp.) and *Taxus* (7 spp.). *Palaeotaxus* Nath., the only fossil genus of the family, has been reported from the Triassic.

DISTINGUISHING FEATURES—The family is characterised by evergreen, slow-growing, profusely-branched, long-lived shrubs or small trees. The acute leaves are spirally arranged on the branches. The leaves gradually taper at the apex to a horny point. Secondary wood is compact and pycnoxylic, possessing tertiary spirals on the walls of tracheids (fig. 8-3). Resin canals are absent in the Taxales. The reproductive organs are very different from those of true conifers. The male flowers occur singly in the axils of foliage leaves or bracts, and are characterised by intermingling of sterile scales with the sporophylls (stamens). The floral axis has a number of decussate scales at the base and above these, the sporophylls are arranged in whorls. These sporophylls may be

1. Coulter, J. M. and C. J. Chamberlain 1910.
2. Florin, R. 1948.
3. Dallimore, W. and A.B. Jackson 1948.
4. Hui-Lin Li 1952.
5. Turrill, W. B. 1959.

radially symmetrical e.g., *Taxus* or dorsiventral e. g., *Torreya, Amentotaxus*. The female flowers occur, in the axils of leaves or leaf scales on secondary fertile dwarf shoots (*Taxus*) or on long-shoots. The ovule, in contrast with the conifers, is borne in direct continuation of the floral axis. Fruits consist of erect bony seeds surrounded by a fleshy aril, the embryo is dicotyledonous.

## *TAXUS* Linn.

SYSTEMATIC POSITION—

Order—*Taxales*

Family—*Taxaceae*

Genus—*Taxus*

The genus *Taxus*, according to Engler and Prantl[1], includes a single species *T. baccata* Linn. Pilger[2] regarded that this species differed widely in habit and foliage in different countries. Dallimore and Jackson[3] include 9 distinct species under this genus viz., *T. baccata* Linn. (with 38 varieties), *T. brevifolia* Nuttall, *T. canadensis* Marshall (with 2 varieties) *T. chinensis* Rehder, *T cuspidata* Siebold and Zuccarini (with 7 varieties), *T. floridana* Chapman, *T. globosa* Schlechtendal, *T. hunnewelliana* Rehder and *T. media* Rehder.

GEOGRAPHICAL DISTRIBUTION—*Taxus* is widely distributed in the Northern Hemisphere. It occurs in North America, England, Europe, China, Japan, Burma, Malaya, North Africa and North India. In India, *Taxus* grows both in the Eastern as well as the Western Himalayas, in the Khasi and Naga hills, and Manipur at an altitude of 1800 metres or more above the sea level. *T. wallichiana* Zucc[4], a narrow-leaved Himalayan form, is specifically not very distinct.

MORPHOLOGICAL FEATURES—*Taxus baccata*, commonly known as the 'yew', is a tall, evergreen tree that grows in the Himalayas. It usually attains a height of 9 to 12 metres and is long-lived. The plant has a columnar trunk with branches

1. Engler, A and K. Prantl 1889.
2. Pilger, R. 1926.
3. Dallimore, W. and A. B. Jackson 1948.
4. Raizada, M. B. and K. C. Sahni 1960.

that grow horizontally to form a dense canopy. The plant possesses a long tap root.

The spirally arranged foliage leaves are 2 to 3 cm long, narrow, flat with prominent midrib and recurved margins (fig. 8-1). The upper surface is shining and dark-green in colour while the lower surface is pale or rusty-red in colour. The scale leaves on the fertile shoots are opposite and decussate and they are shortly petioled. Leaf-bases are persistent and they appear to form ridges on the shoot. Leaf apex is sharply pointed because of the accumulation of mineral crystals.

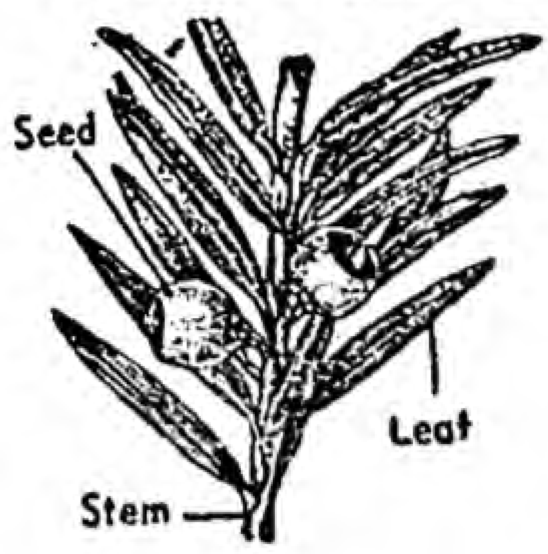


Fig. 8—1 A twig of *Taxus baccata* with leaves and seeds (After Wettstein).

HISTOLOGICAL FEATURES—Histologically the stem of *Taxus* resembles with that of *Pinus* in many respects. It possesses a thick cuticle, a single-cell thick epidermis, sclerenchymatous hypodermis and multilayered cortex. Vascular bundles are arranged in a ring, they are conjoint, collateral and open (fig. 8-2). Protoxylem

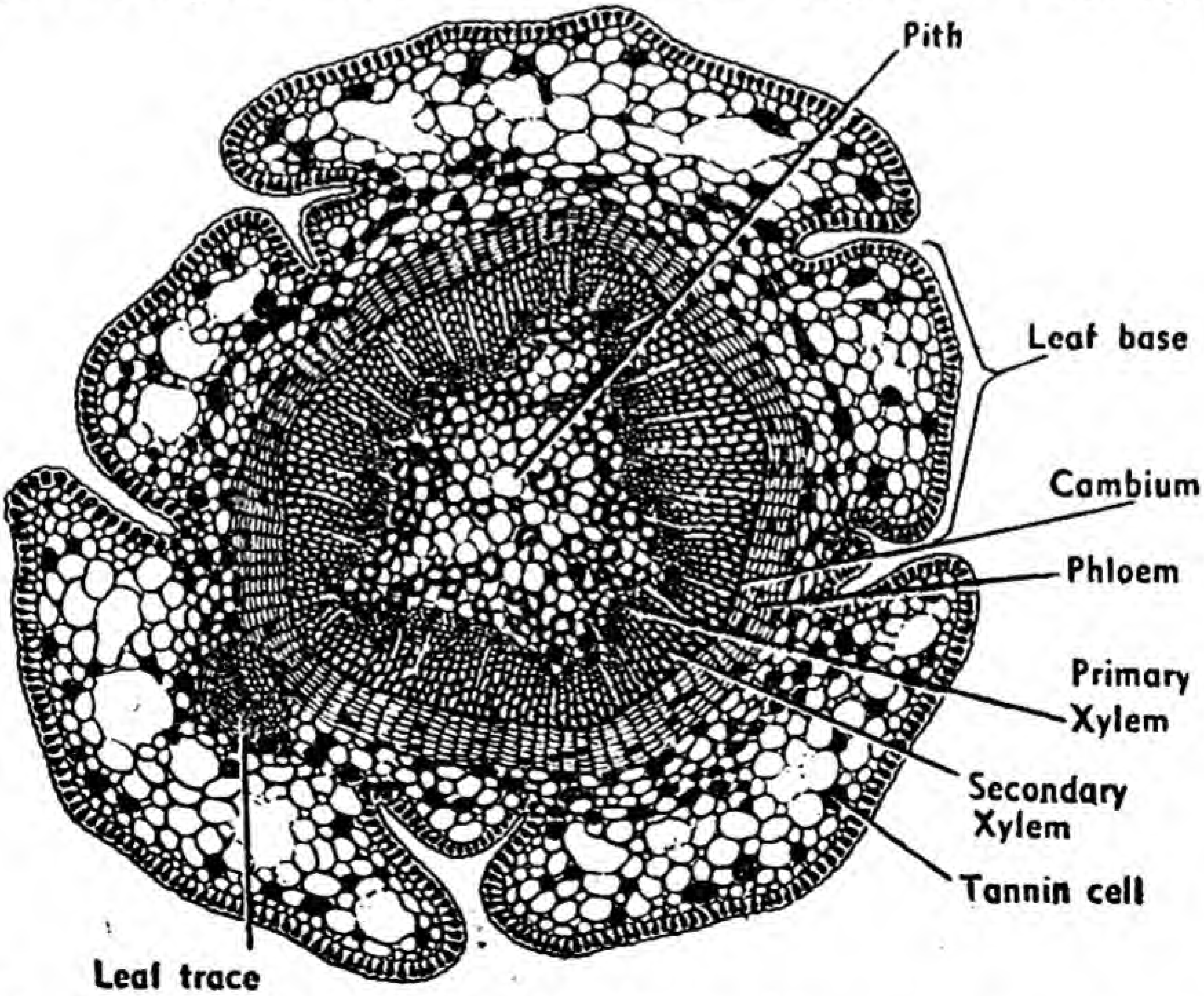


Fig. 8—2 T. S. of the stem of *Taxus baccata* with secondary tissues and a single leaf trace.

is endarch and is made up of tracheids. Phloem consists of sieve cells and phloem parenchyma. Pith is small and is situated in the centre. Secondary growth is initiated by the activity of the cambium present in the vascular bundles, which cuts off secondary xylem and secondary phloem on the inner and the outer sides respectively. Xylem rays are narrow and homogenous. Extra-steler secondary growth takes place by the activity of phellogen or cork cambium. It cuts off phellem on the outer and phelloderm on the inner sides.

The stem of *Taxus* differs from that of *Pinus* in the absence of the resin canals. Further, the tracheids of the secondary wood of *Taxus* possess spiral thickenings (fig. 8-3).

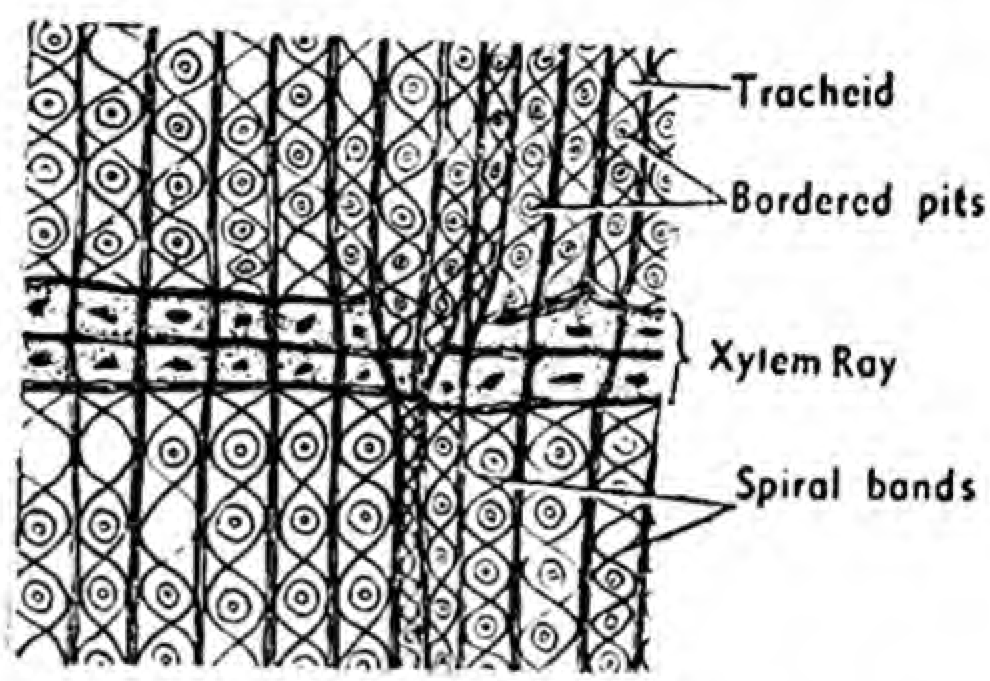



Fig. 8—3 R. L. S. of the wood of *Taxus baccata* showing a biseriate medullary ray and spiral bands of thickenings on the tracheids.

The root of *Taxus* is diarch; it lacks resin canals, otherwise, it resembles the root of *Pinus*.

The leaf of *Taxus* is dorsiventral. It is surrounded by a thick cuticle on the dorsal and the ventral surfaces (fig. 8-4). Stomata are sunken in pits and occur only on the lower

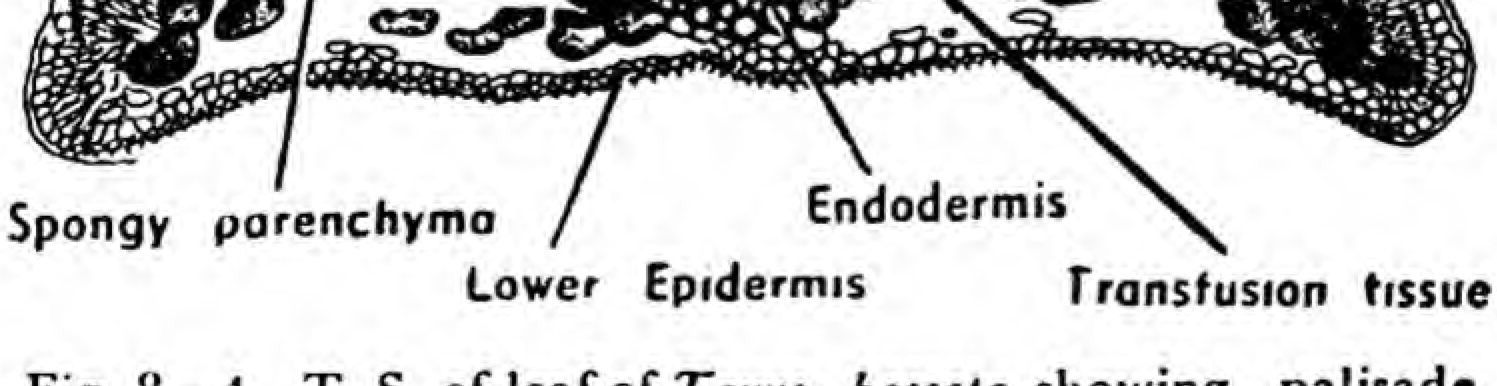



Fig. 8—4 T. S. of leaf of *Taxus baccata* showing palisade and transfusion tissues.

surface of the leaf. Resin canals are absent. The mesophyll is differentiated into palisade and spongy parenchyma. A single

vascular bundle, which constitutes the midrib, is situated in the centre of the leaf. Lateral veins are absent but transfusion tissue occurs on either side of the vascular bundle (fig. 8-4).

## LIFE-HISTORY

The plants of *Taxus* are dioecious, i.e., the staminate strobili and the ovules arise on two different plants. But for the reproductive structures, which become prominent in the months of February and March, the male and the female plants are otherwise similar.

**Male flowers**—The male flowers, usually yellowish in colour, arise in the axils of foliage leaves[1]. They arise in stalked globose heads from the axils of the leaves on the undersides of the branchlets of the previous year. Each male flower consists of 6 to 14 stamens with short filaments, anther scale peltate[2].

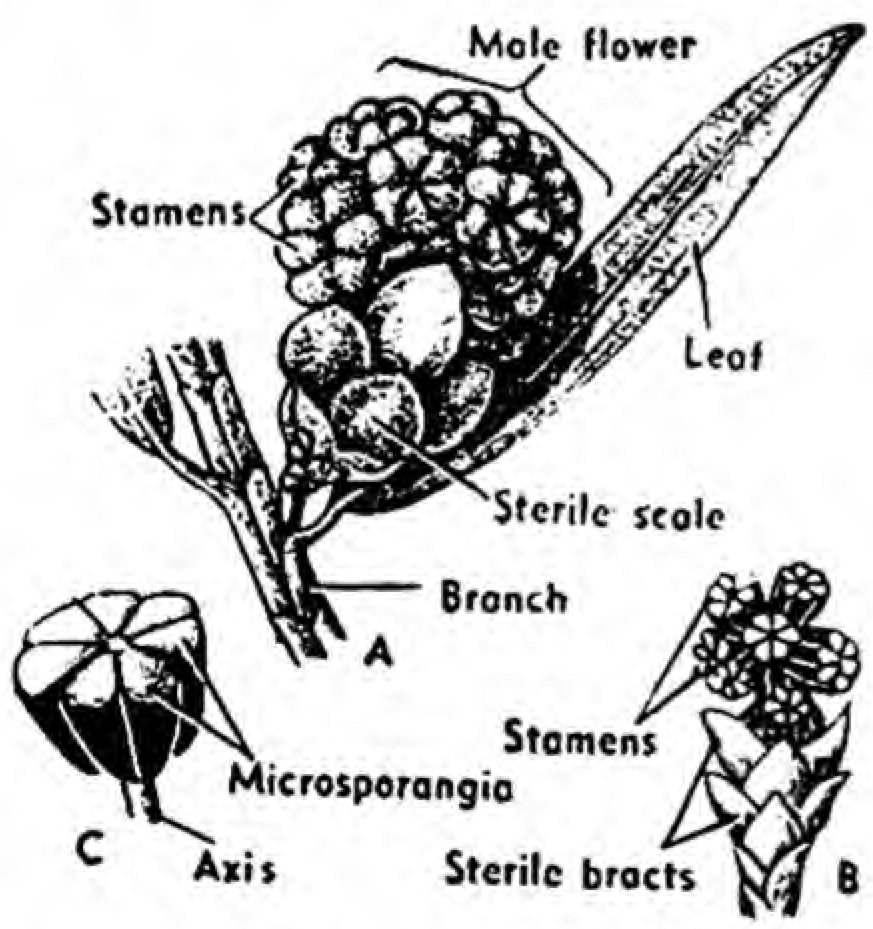



Fig. 8—5 Male reproductive organs of *Taxus baccata* A—a branch with a male flower possessing stamens (microsporangiophores) and sterile scales (After Wettstein); B—a male flower shown detached from the plant (After Beissner); C-a stamen (microsporangiophore) with pendant microsporangia(After Beissner).

The stamen at its apex bears 6 to 8 peltate anthers or microsporangia (fig. 8·5A to C). Dupler[3] observed that in *T. canadensis*, the flower buds possess a broad apex, a character in which they differ from the vegetative buds.

**Stamen**—Each stamen (= microsporangiophore) consists of a short stalk below and peltate shield-like apex above (fig. 8-5B). On the underside of the shield there arise 6 to 8 anthers (= pollen sacs) which are united to one another and to the stalk of the stamen (fig. 8-5C & 8-6). Pollen grains ( = microspores) are released by the break-

1. Florin, R. 1948.
2. Dallimore, W. & A. B., Jackson 1948.
3. Dupler, A. W. 1919.

ing open of the wall of the pollen sac nearest the axis. Dispersal of pollen grain takes place by wind.

The wall of the microsporangium is two-layered. Tapetum develops from the peripheral layer of the sporogenous tissue. The epidermis of the microsporangium is thin-walled at the base. Dehiscence of the microsporangium occurs by the rupture of its cells on maturity (fig. 8-6) and by the elongation of the stalk of the stamen (microsporangiophore). This elongation results in the pushing up of the stamens beyond the bract scales (=scale leaves).

**Microsporogenesis**—The archesporial initials are hypodermal in origin[1]. The number of these initials varies from 4 to 8. The development of microsporangium is eusporangiate. Microspore mother cells (=pollen mother cells) are formed in the month of October in *T. canadensis* and as a result of meiotic division, microspores (= pollen grains) mature two weeks later.

**Vascular supply of the male strobilus**—The vascular bundles supplying the male or staminate strobilus are collateral and endarch but as they reach the apices they become mesarch, occasionally indicating even exarch position[1]. The terminal portions of the vascular bundles are concentric.

**Female (ovulate) strobili**—These arise in the axils of leaves early in one season and mature in the next. The female strobilus consists of a short primary axis bearing a closely imbricated succession of sterile scale leaves (fig. 8-7A&B). From the axils of the upper three scale leaves arise the secondary axes or fertile ovuliferous shoots (flowers).

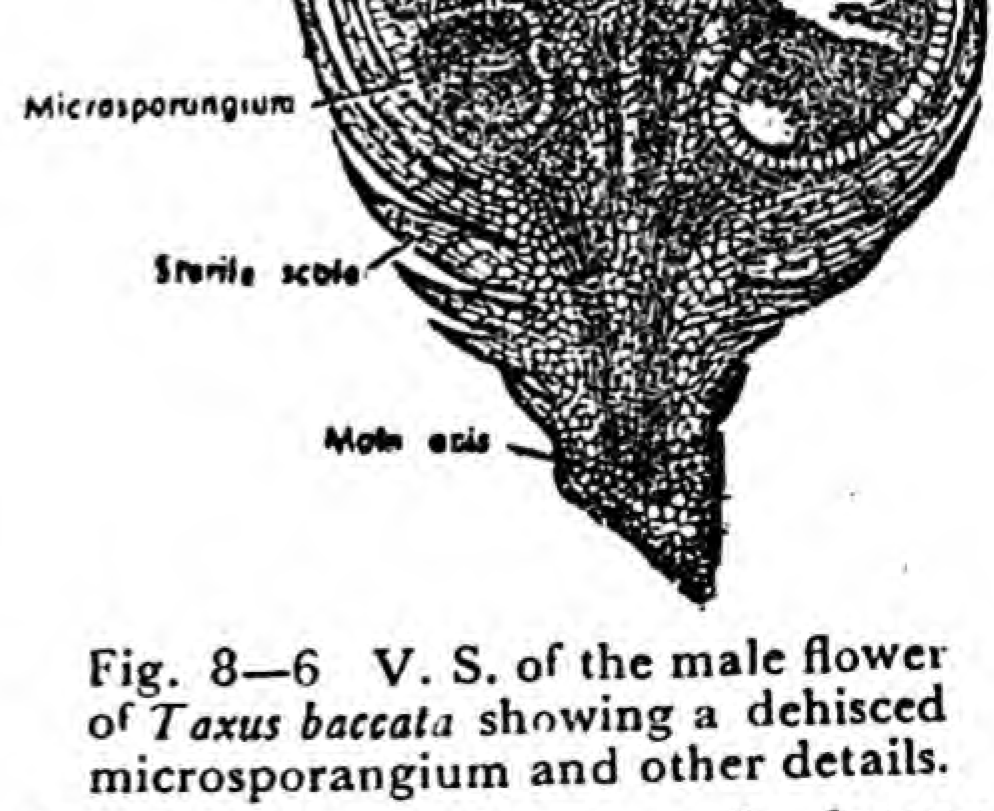



Fig. 8—6 V. S. of the male flower of *Taxus baccata* showing a dehisced microsporangium and other details.

1. Dupler, A. W. 1919.

Dupler[1] regards the primary axis as a vegetative branch of limited growth bearing only reproductive or secondary axes. The primary axis persists and is functional for several seasons. The secondary axis or fertile shoot (female flower) bears 3 pairs of decussate scale leaves and a terminal ovule (fig. 8-7B). The lower pair of scale leaves is at right angles to the subtending bract. The growth of the apex of the primary shoot is usually suppressed but occasionally it proliferates after the formation of the seed and produces a secondary axis bearing an ovule in the coming year (fig. 8-7 F).

**Ovule (megasporangium)**—The ovule bears two lateral ridges. It is a round or oval structure. The number of ridges may rarely increase to 3 or 4[2]. The ovule is surrounded by a thick envelope which forms a long micropylar canal above the nucellus (fig. 8-7D).

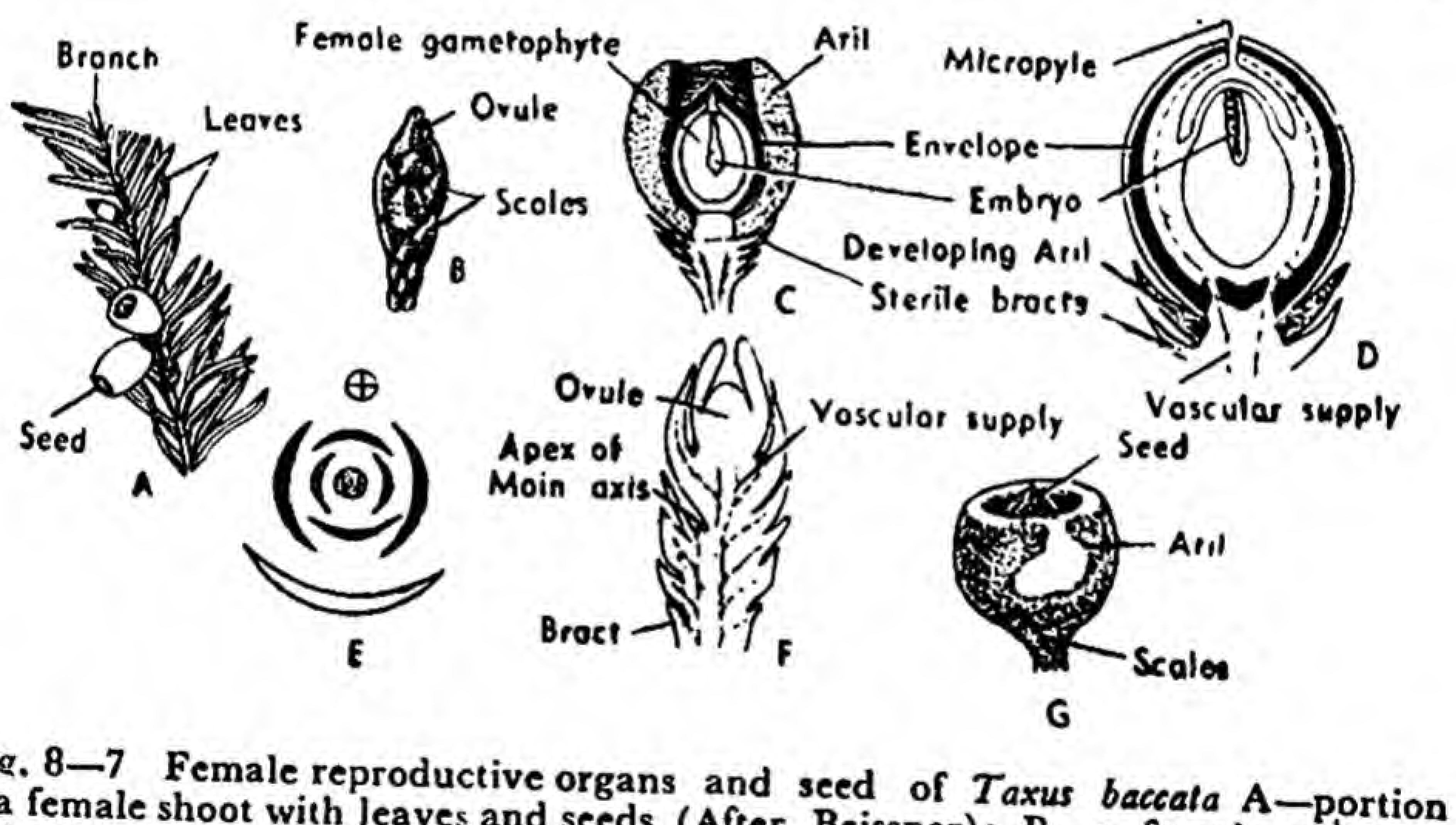



Fig. 8—7 Female reproductive organs and seed of *Taxus baccata* A—portion of a female shoot with leaves and seeds (After Beissner); B—a female strobilus with a terminal ovule (After Wettstein); C—L. S. of the mature seed (After Beissner); D—L. S. of the ovule before the growth of aril (After Sahni); E—Floral diagram of a female flower (After Wettstein); F—L. S. of the female shoot with a young ovule and its vascular supply (After Hirmer); G—an entire seed with aril and scales (After Wettstein).

At the base of the envelope arises a greenish saucer-shaped outgrowth about the time of pollination of ovule, it becomes fleshy, red and cup-shaped. This outgrowth later surrounds the entire ovule and is commonly called an 'aril' or a 'cupule' (fig. 8-7C,

1. Dupler, A. W. 1920.
2. McLean, R. C. & W. R. Ivimey Cook 1962.

D & G). The morphological nature of the cupule is controversial. Some morphologists consider it to be the second covering of the ovule like the 'epimatium' of the Podocarpaceae, while others regard it as an outermost part of the envelope or integument.

**Vascular supply of the ovule**—The ovule receives its vascular supply directly from the axis. The vascular bundles of the envelope penetrate the stony layer at its base. Two bundles after penetrating the stony layer bend into a thickened knee-like flexure. Sahni[1] pointed out that the flexure was a place at which the vanished nucellar strands were formerly given off in the Cordaitales (fig. 8-7D).

**Megasporogenesis**—The archesporial initial is hypodermal in origin and archesporial tissue can be easily recognised when the ovule is young. The initial divides periclinally to form a primary wall cell and a primary sporogenous cell; the latter by repeated divisions forms a considerable mass of sporogenous tissue. Only the lowermost one or rarely two cells of this sporogenous tissue function as megaspore mother cells. Each megaspore mother cell divides meiotically to form a linear tetrad of 4 cells, the lowermost cell developing into a female gametophyte (=embryo sac). The upper three cells usually disorganise. In rare cases two female gametophytes may be produced in the same ovule.

**Pollination**—It usually takes place in the month of March. Uninucleate microspores (=pollen grains) are shed from the microsporangium fig. 8-8 A). The microspores after dispersal by wind reach the apex of the micropyle. The latter secretes a drop of fluid, 'the pollination drop' for catching them. The pollen grains are sucked inside and a little later they germinate. The exine of the microspore ruptures and the intine grows out as a pollen tube (fig. 8-8 D & F). This penetrates through the tissue of the nucellus when the archegonia are organised.

GAMETOPHYTIC GENERATION—The microspores and the megaspores represent the earliest stages of the male and the female gametophytic generations respectively.

1. Sahni, B. 1920.

**Male gametophyte**—Microspores are formed in autumn or in early spring and they are uninucleate when shed. Each microspore is protected by two walls, the outer thicker is called the exine, and the inner thinner, the intine (fig. 8-8A&B). The pollen tube penetrates the nucellus rapidly and enlarges. The microspore nucleus divides to form two cells, the lower of these is called the tube cell and the upper one, the generative cell (fig. 8-8C).

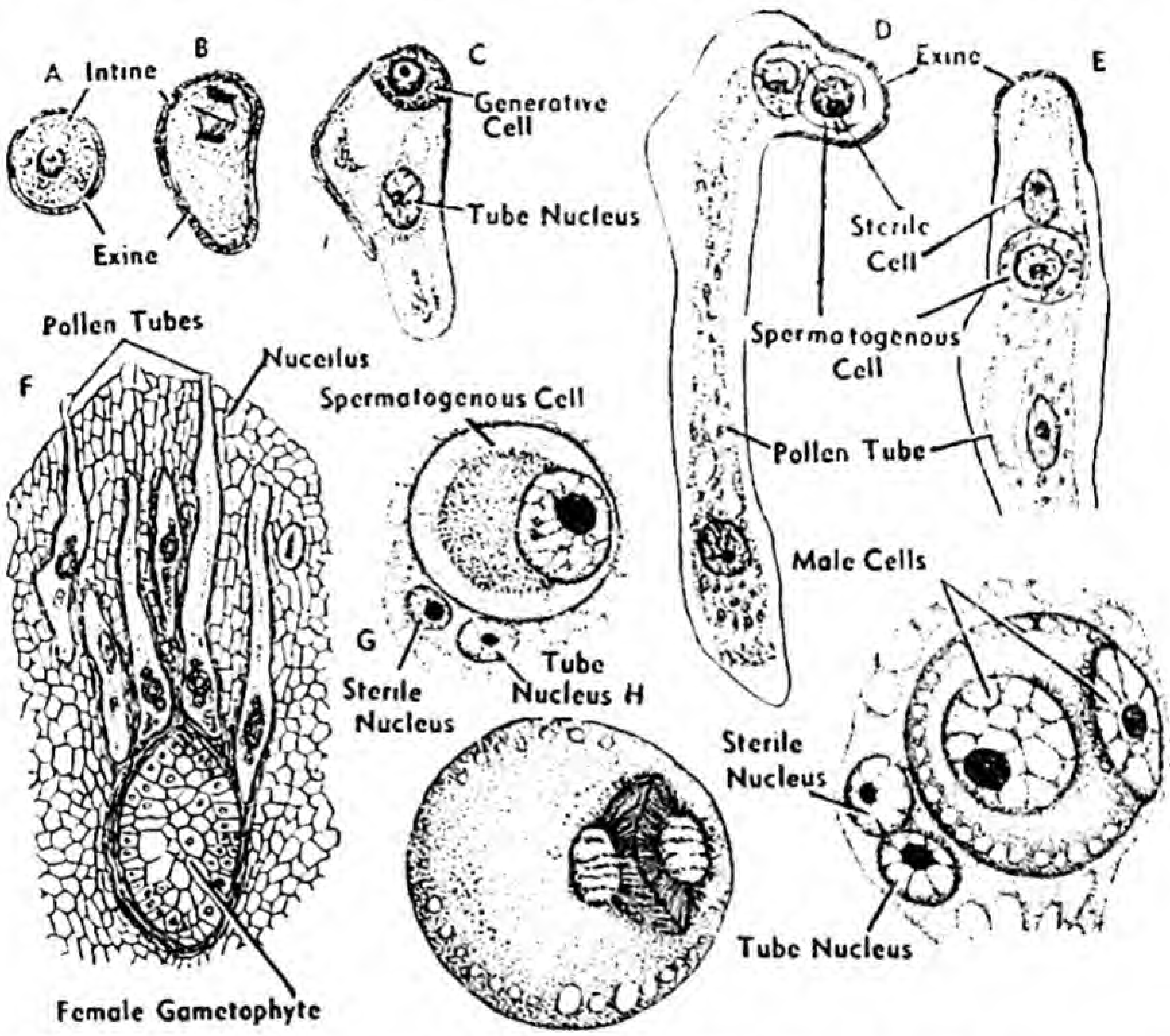



Fig. 8—8 Development of male gametophyte in *Taxus canadensis* A—a mature microspore at the time of shedding; B—first division of microspore; C—formation of a generative cell and a tube nucleus; D—division of the generative cell into a spermatogenous cell and a sterile cell and the elongation of the pollen tube; E—movement of the sterile and spermatogenous cell into the pollen tube; F—portion of an ovule with female gametophyte and pollen tubes in the nucellus; G—a mature spermatogenous cell with the sterile and tube nuclei; H—spermatogenous cell dividing; I—two unequal male cells formed by the division of the spermatogenous cell (After Dupler).

Prothallial cells have not been observed in *Taxus*. The generative cell later divides into a sterile cell and a spermatogenous cell (fig.8-8D&E). The spermatogenous cell finally forms two unequal male cells (fig. 8-8H-I). Thus only three divisions take place in the development of the male gemetophyte of *Taxus*. The unequal

male cells (=gametes) are nonflagellate. The tube cell, sterile cell and the two unequal male gametes all may be present at the tip of the pollen tube at the time of fertilization (fig. 8-8).

Sterling[1] suggested the following scheme for the development of male gametophyte in *Taxus*.

Embryonal cell
(functioning as antheridial initial)

Generative ce l — Tube cell

Spermatogenous cell (=body cell) — Sterile cell (=stalk cell)

Male cell (gamete) — Male cell (gamete)

**Female gametophyte**—The nucleus of the female gametophyte (=embryo sac) undergoes free nuclear divisions. According to Sterling[2], in *T. cuspidata* free nuclear stage of the female gametophyte is characterized by the assumption of a flask-shaped form of the sac and the aggregation of most of the nuclei and cytoplasm at its basal end. The wall formation is initiated at 256, free-nuclear stage and proceeds by means of open ingrowing alveoli. Dupler[3] observed in *T. canadensis* that after free nuclear stage radial walls are formed before the periclinal ones which close the cavity (fig. 8-8F). The cells of the female gametophyte are uninucleate in the beginning but become multinucleate afterwards. Archegonia appear later in the female gametophyte towards the micropyle. Their number varies from 5 to 11 in *T. baccata*, 4 to 8 in *T. canadensis*, 6 to 25 in *T cuspidata*. This number varies from 4 to 25 in other species. The neck of the archegonium is made up of 2 to 4 cells. Often the gametophytic tissue proliferates round the archegonia; thus the archegonia become seated in deep pits. Each archegonium consists of a neck and a venter. The venter possesses a central cell (= egg) and probably no ventral canal nucleus. The

1. Sterling, C. 1963.
2 Sterling, C. 1948.
3. Dupler, A. W. 1917.

nutritive jacket round the archegonium is indistinctly differentiated according to Sterling.[1]

**Fertilization**—It usually takes place about 1 to 2 months after the pollination. As the archegonia mature, the pollen tubes lying in close vicinity in the hollow cavity, rupture and liberate the two unequal male cells. Only the larger of the two male cells, according to Dupler[2], fuses with the egg or the central cell and forms the zygote. The other smaller male cell, the tube cell and the stalk cell ultimately degenerate.

DEVELOPMENT OF THE EMBRYO—Several archegonia in an ovule may be fertilized but only one generally develops into an embryo (fig. 8-7C). Without undergoing a period of rest the zygote undergoes free nuclear divisions. Wall formation begins after 32-nucleate stage and a proembryo is formed. The cells of the proembryo divide further and get arranged in three tiers; the lowest tier of 6 to 14 cells forms the embryo while the middle one of 9 to 13 cells forms suspensors. The cells of the middle and upper tiers elongate considerably pushing down the embryonal tier into the endosperm or the female prothallus. The uppermost or open tier is made up of 9 to 13 cells.

The mature embryo is straight and dicotyledonous. It consumes the entire endosperm during its development hence the seed becomes non-endospermic. Simple polyembryony may occur when more than one archegonia are fertilized but cleavage polyembryony is not known.

**Structure of the seed**—The seed of *Taxus* (figs.8-1&8-7A) is protected by a three layered seed-coat. The outermost layer is thin and brown, which soon detaches. The middle layer is hard and stony and the innermost is fleshy. The ripe seed is invested by a scarlet-red aril or cupule (fig. 8-7G).

**Germination of the seed**—The seed germinates into a seedling possessing two linear cotyledonary leaves which are larger than

1. Sterling. C. 1948.
2. Dupler, A. W. 1917.

the normal foliage leaves. The foliage leaves arise in the coming year and are traversed by a single vascular bundle.

## OTHER GENERA OF TAXACEAE

*Torreya* occurs in California, W. Florida, China and Japan. *Amentotaxus* is found in Western China and Assam. *Austrotaxus* and *Nothotaxus* (= *Pseudotaxus* Cheng) are monotypic and are found in New Caledonia and China respectively.

Chapter 9

# Gnetales

GENERAL CHARACTERS—The Gnetales include woody plants which are regarded to be the most highly evolved amongst the gymnosperms. They resemble the angiosperms in certain morphological and histological features but in the absence of an ovary, style and stigma and in their method of pollination they are still gymnospermous. Further, in the Gnetales true fruits are not formed as in the angiosperms. The Gnetales possess characters which are enumerated below :

The plants are either xerophytic or mesophytic. *Welwitschia* occurs in desert, *Ephedra* in arid situations and *Gnetum* in humid and tropical regions. Leaves are opposite, simple, elliptical, (*Gnetum*), strap-shaped (*Welwitschia*) or reduced to scales (*Ephedra*). Xylem consists of tracheids and true vessels which are sometimes quite elaborate. The strobili are compound and resemble angiospermous inflorescence. Female flowers possess a single erect ovule. The male flowers possess perianth and anthers. Perianth is distinct and occurs in one or two whorls. Pollination is mostly anemophilous, sometimes doubtfully entomophilous as in *Gnetum*. The male cells are passively carried through a pollen tube, i. e., the fertilization is siphonogamous. The endosperm starts developing before fertilization and is still haploid unlike that of the angiosperms where it is a post-fertilization product and is generally triploid. The embryo possesses two cotyledons.

CLASSIFICATION—The order Gnetales[1] is divided into three families, viz., the Ephedraceae, the Welwitschiaceae and

1. Markgraf, Fr. 1926

the Gnetaceae, and each family has a single genus, *Ephedra*, *Welwitschia* and *Gnetum* respectively. Eames[1] has raised the above three families to the rank of orders and calls them Ephedrales, Welwitschiales and Gnetales.

## *EPHEDRA* L[2].

SYSTEMATIC POSITION—

Order—*Gnetales*.

Family—*Ephedraceae*

Genus—*Ephedra*. Tourn ex. L.

Eames[3] places *Ephedra* under the family Ephedraceae. Pant[4] keeps *Gnetum* and *Welwitschia* together under the division Chlamydospermophyta of Pulle but places *Ephedra* separately under the Coniferophyta.

GEOGRAPHICAL DISTRIBUTION—*Ephedra* is widely distributed in both the Eastern as well as the Western Hemispheres. It grows in the Southern part of North America, central part of South America, North Africa, Portugal, Spain, Germany, France, Italy, Iran, China, Baluchistan, Afghanistan, etc. *Ephedra foliata* var. *ciliata* grows wildly as a scandent shrub climbing over small trees in the southern part of the Punjab planes and Rajasthan. It is generally cultivated in gardens in other places.

HABIT—*Ephedra* includes nearly 35 species of which about 6 occur in India. The plants are xerophytic shrubs. *E. foliata* Boiss. attains a height of about six metres and it thrives well in arid climate. A few species are climbers. *E triandra* Tul. attains a tree-like habit under favourable conditions.

DISTINGUISHING FEATURES OF THE INDIAN SPECIES—Species of *Ephedra* which occur in the North-West Himalayan region are all shrubby except *E. foliata* which is a

1. Eames, A. J. 1952.
2. Willis, J. C. 1966
3. Eames, A. J. 1952.
4. Pant, D. D. 1957.

Lindley

climber. The shrubby species may be identified as under[1] :

Tubillus twisted

Seed 2 to 3 mm long ; bracts of female strobilus connate in the lower one-third... *E. pachyclada* Boiss.

Seed 5 to 6 mm long ; bracts of female strobilus connate in the lower two-thirds . *E. intermedia* Schrenk et (C. A. Mey) var. *tibetica* Stapf.

Tubillus straight

Tubillus not more than 1 mm long

Strobilus 10 mm long ; seeds 4 to 6 mm long ; tubillus 0.5 mm long ..*E. saxatilis* Royle var. *sikkimensis* (Stapf.) Florin.

Strobilus 5 to 8 mm long; seeds 4 to 6 mm long; tubillus 1.0 mm long... *E. gerardiana* Wall.

Tubillus 1.5 to 3.5 mm long.

Branches very smooth ; strobilus 5 to 7 mm long ; seeds 4 to 7 mm long . *nebrodensis* Tin. var. *procera* Stapf.

Branches smooth or scaberulous; strobilus 7 to 10 mm long; seeds 3.5 to 4.5 mm long...*E. regeliana* Florin.

Ephedra

MORPHOLOGICAL FEATURES—The plant has a profusely branched stem. In young stages the stem and branches are green. Leaves are small, scale-like and inconspicuous (fig. 9-1A& B). They usually arise in opposite and decussate manner but in a few species they may be arranged in whorls of mostly three (rarely four) at each node. Scale leaves are united at the base to form a basal sheath. Branches usually arise from the axils of leaves.

HISTOLOGICAL FEATURES—The leaves are much reduced, therefore, the stem is the main photosynthetic organ. The outer surface of the stem is ridged. Stomata occur in the furrows between the ridges and are deeply sunken in pits. Epidermis is thick-walled and is covered over by a thick cuticle (fig. 9-2). At the ridges, groups of fibre cells are present in the hypodermal region. The cortex is differentiated into an outer palisade layer and an inner spongy tissue. The cells of both these regions possess chloroplasts. Cortex is followed by a single cell thick endodermis in young stages. Pericycle is not distinct. Vascular bundles are

1. Bor, N. L. 1953.

vascular

arranged in a ring (fig. 9-2). They are endarch and collateral. Cambium is present between the xylem and the phloem. Pith is usually parenchymatous but at nodal regions, it is lignified to form transverse plates. Each internode usually possesses 2 pairs of leaf-trace bundles and 4 stem bundles (total 8). Each leaf, according to Marsden and Steeves[1], is supplied with 2 leaf trace bundles. There is thus a double leaf-trace similar to that of the pteridosperms. In *Ephedra* the root is usually diarch.

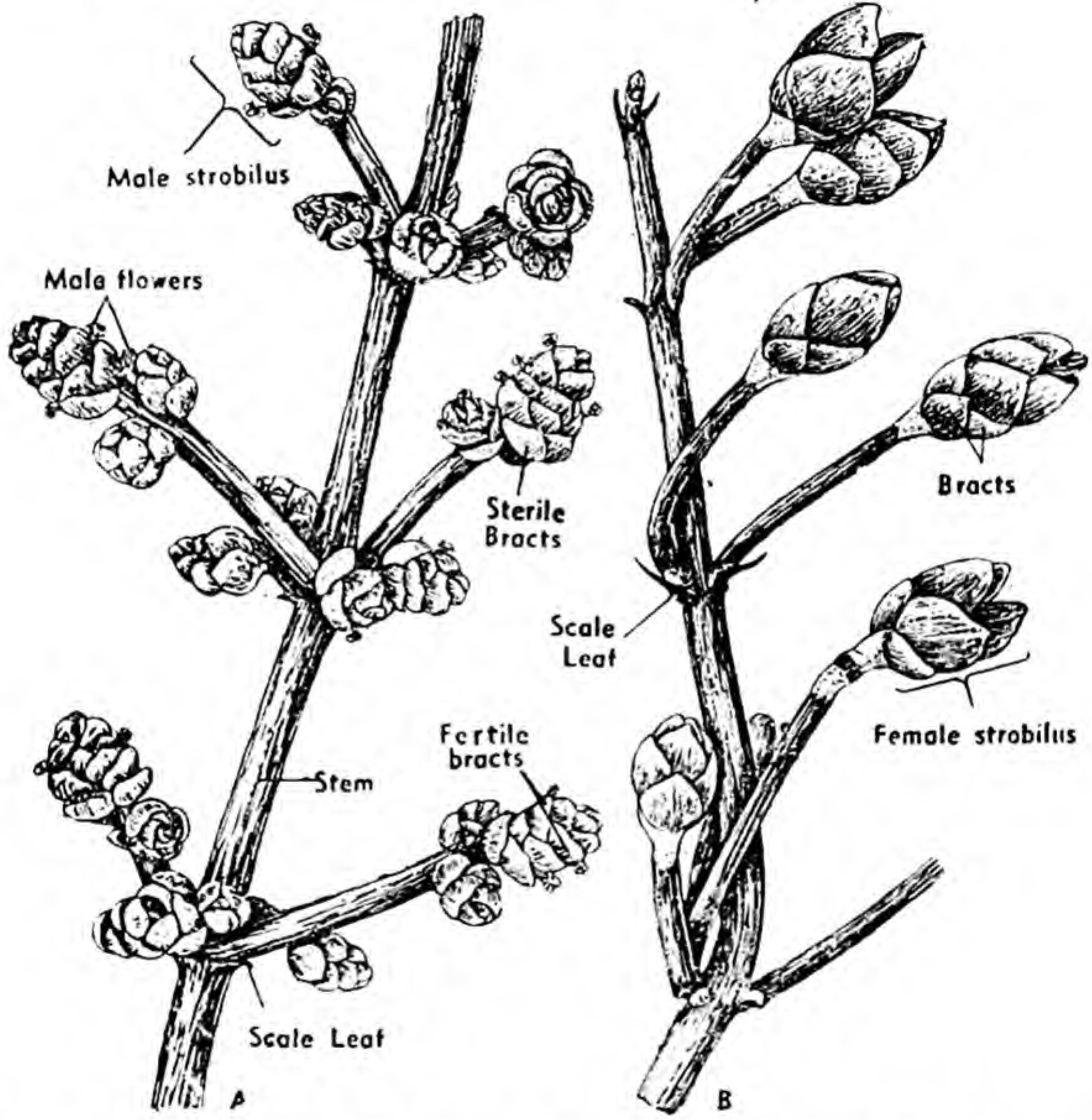



Fig. 9—1 *Ephedra sp.* with scale leaves and reproductive organs A—A twig with male strobili; B—A twig with female strobili. (After Foster and Gifford).

**Secondary growth**—Secondary growth takes place as a result of cambial activity. Annual rings are formed in the secondary wood. Xylem rays when young are thin and uniseriate ~~(fig. 9-2)~~ but they become multiseriate and broad when old. Tracheids have

1. Marsden, M. P. F. and T. A. Steeves 1955.

a single row of bordered pits with crassulae on their radial as well as on the tangential walls. Transitional stages showing the evolution of vessels from tracheids can also be observed. These stages point out an independent origin of vessels in *Ephedra*.[1] Vessels are quite abundant (fig. 9-2 & 3) in the spring wood, though they are scarce in the autumn wood. A few cells with stellate crystals of calcium oxalate are also present. Outside the secondary phloem arises the phellogen in the third or fourth year of the growth of the plants.

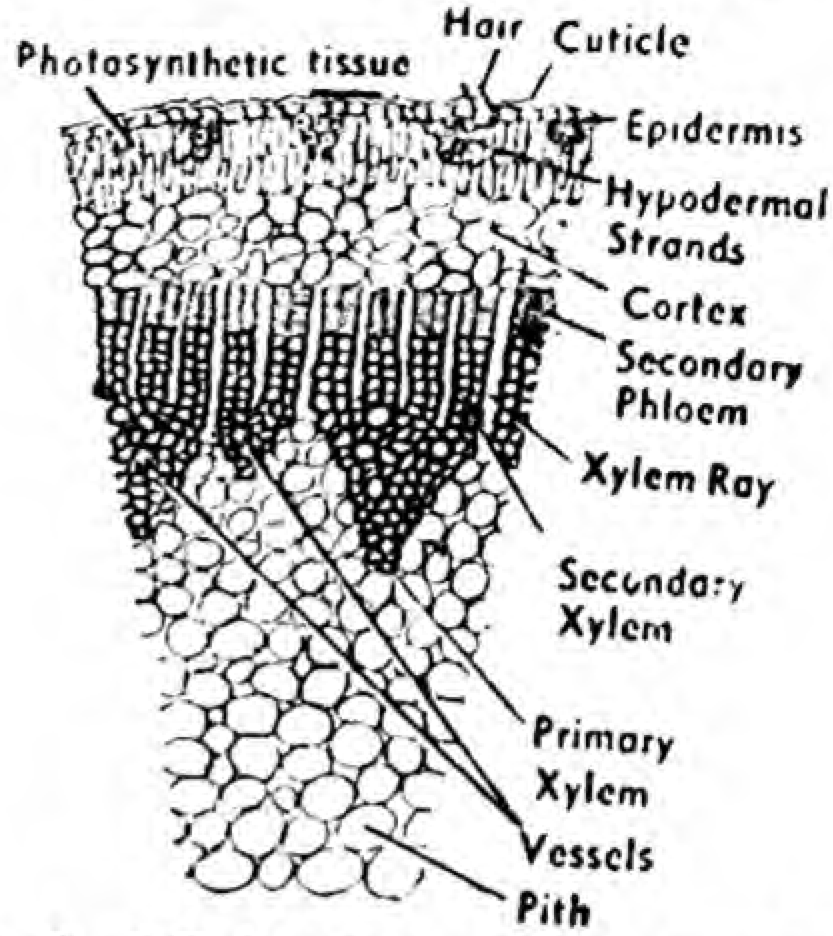


Fig. 9—2 T. S. of stem of *Ephedra foliata* with secondary growth.

The leaves of *Ephedra* have double leaf-trace like those of the Pteridosperms and *Welwitschia*. Marsden and Steeves[1] observed that the two traces are related to a single gap. The development of stomata in *Ephedra* is haplocheilic which is in contrast to that of other two genera where it is syndetocheilic. In *G. gnemon*, Maheshwari and Vasil[2] have observed both the types of development (fig. 9-17).

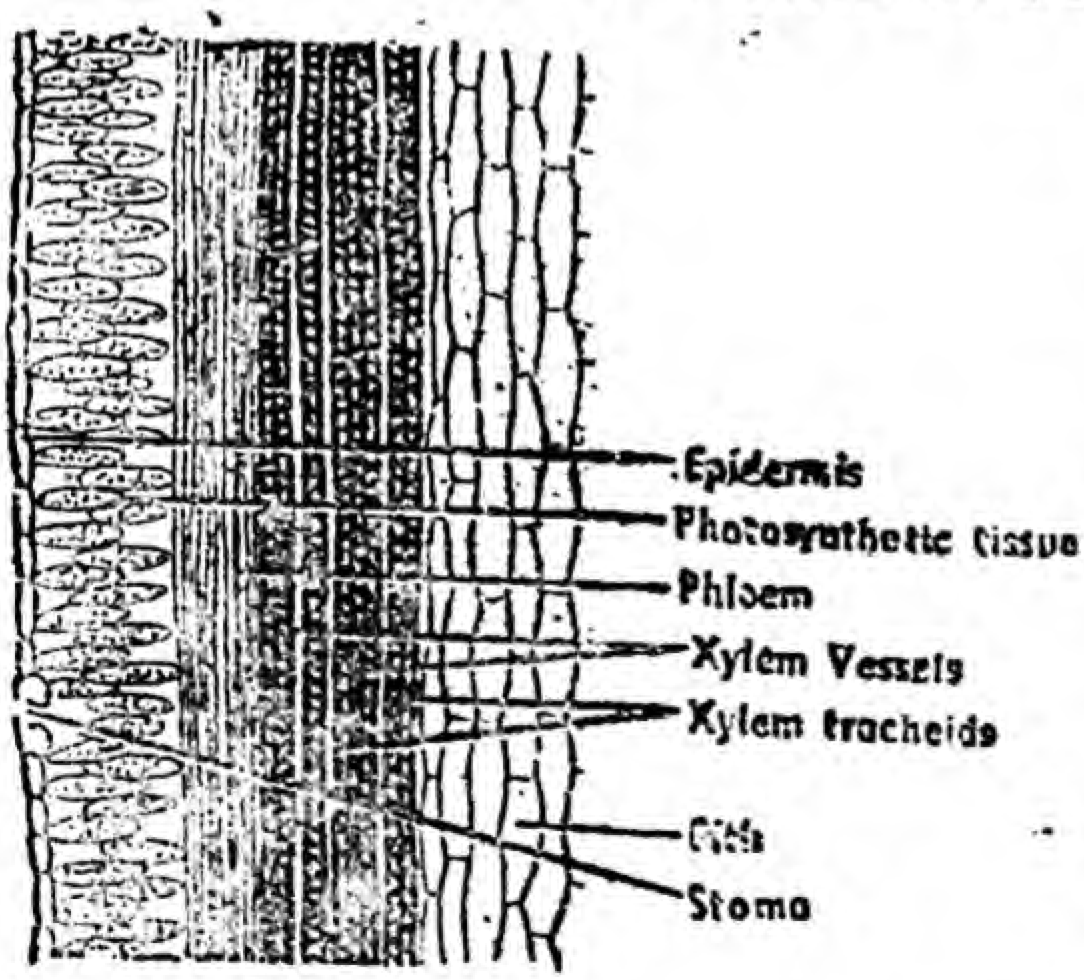


Fig. 9—3 R. L. S. of stem of *Ephedra foliata* (diagrammatic).

SHOOT APEX—In *E. fragilis* Desf. var. *campylopoda* (Seeliger)[3] and *E. altissima* Desf. (Gifford)[4] observed the well-marked

1. Marsden, M. P. F. & T. A Steeves 1955.
2. Maheshwari, P. & V. Vasil 1961.
3. Seeliger, I. 1924.
4. Gifford, E. M. 1943.

tunica layers in their shoot apices. The shoot apex in *Ephedra*, like that of *Gnetum*, is thus relatively advanced over that of the other gymnosperms and points towards the angiosperm-like condition.

## LIFE-HISTORY

*Ephedra foliata* and other species of *Ephedra* are dioecious. Pearson[1] observed a few instances where male and female strobili were borne on the same plant; Eames[2] regards these as 'monstrosities'.

**Male strobilus**—The male or microsporangiate strobili develop in the axils of leaves (fig. 9-1 A). They arise in whorls of 2, 3 or 4 from the nodes of branches. Each strobilus possesses a central axis on which are borne 2 to 8 pairs of opposite and decussate bracts. The lower one or two bracts of the male strobilus are sterile while the upper ones are fertile (fig. 9-1 A). In the axils of the fertile bracts arise the male flowers. Usually only one male flower arises in the axil of a bract.

**Male flowers**—Each male flower is axillary and consists of an axis (= antherophore) and a pair of thin opposite scales. The scales (= bracteoles) have been interpreted as 'perianth'. The axis at its apex bears 1 to 8 anthers (=microsporangia). The floral axes of *E. distachya* Linn. and *E. intermedia* Schrenk have been regarded as primitive by Eames[2]. He also believes that the axis is formed here as a result of the fusion of a pair of microsporophylls.

**Microsporangia**—The microsporangia or anthers, situated at the apex of the antherophore, have also been referred to as 'synangia'. They possess 2 to 3 loculi. Each loculus opens through a terminal slit to release the microspores or pollen grains.

**Female strobili**—The female or megasporangiate strobili also arise in whorls of 2, 3 or 4 in the axils of the leaves at each node (fig. 9-1 B). Each female strobilus is an elongated structure pointed at its apex. It consists of a central axis with 2 to 4 or more pairs of opposite decussate bracts (fig. 9-1 B & 9-6 A). The bracts in a few species of *Ephedra* are swollen and juicy. Most of the bracts are sterile except the apical one or two, which bear a single female flower in their axil.

1. Pearson, H. H. W. 1929.
2. Eames, A. J. 1952.

**Female flowers**—Each female flower possesses a short stalk, which at its apex bears an ovule or a megasporangium. Each flower arises in the axil of a fertile bract.

**Megasporangia**—The megasporangium or the ovule consists of a centrally-situated nucellus enclosed by a two-layered envelope (fig. 9-6 B). Ontogenic studies and vascular anatomy reveal that the outer layer of the envelope is equivalent to a pair of fused bracts. Eames[1], therefore, advances a hypothesis that the ovule in *Ephedra* is borne at the apex of a much reduced basal megasporophyll which is surrounded by a pair of bracts (fig. 9-6 A).

**Microsporogenesis**—Land[2] in *E. trifurca* Torr. and Maheshwari[3] in *E. foliata* studied the development of the microspores. According to these authors, the archesporial cells are hypodermal in origin like ~~those of the conifers.~~ The archesporial cells, as a result of periclinal divisions, form the primary parietal cells and the centrally-situated primary sporogenous cells. A single cell thick wall layer is cut off from the primary parietal cells, which also give rise to tapetum. The primary sporogenous cells ultimately form microspore mother cells. During the formation of microspores the tapetal cells become 2 to 4 nucleate. The microspore mother cells, ~~as a result of~~ meiotic divisions, form microspores. Each microspore possesses two walls ; the outer thick wall is called the exine and the inner thinner one, the intine. Microspores are boat-shaped and unwinged. The pollen grains or microspores are released through a terminal slit present in the microsporangium.

**Megasporogenesis**—The ovule in the young stage consists of a centrally-situated nucellus surrounded by a two-layered envelope. At maturity, the inner layer, for about a half of its length from the base, fuses with the nucellus while the upper half remains free; this part elongates to form a long micropylar canal ~~(fig. 9-6 B & C)~~. The archesporial cell (=functional megaspore mother cell), ~~according to Maheshwari[3],~~ is hypodermal in origin ~~(fig. 9-4 A & B)~~. This cell divides periclinally and cuts off several parietal or wall cells. As a result of these divisions, the megaspore mother cell comes to lie deeper within the nucellar tissue. The megaspore mother cell divides meiotically to form a linear or 'T' shaped tetrad of megaspores ~~(fig. 9-4 C)~~, the lowest cell of the tetrad develops into a female gametophyte (fig. 9-4 D).

1. **Eames, A. J. 1952.**
2. **Land, W. J. G. 1904.**
3. **Maheshwari, P. 1935.**

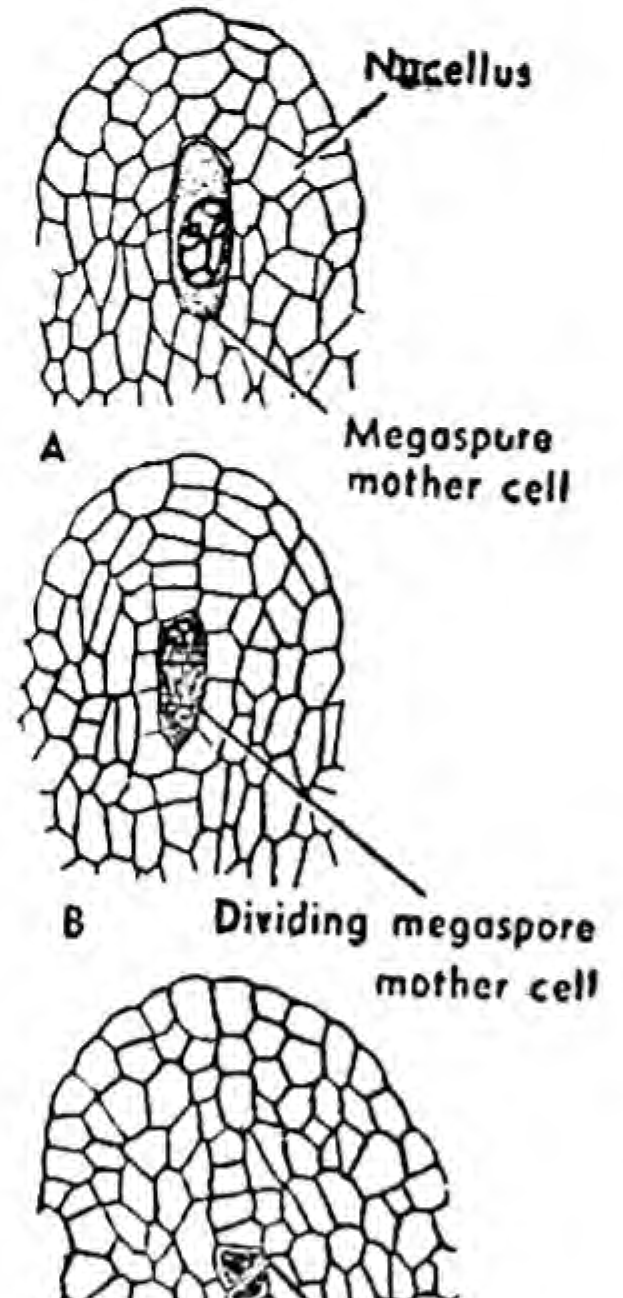



Fig. 9—4 Megasporogenesis and female gametophyte of *Ephedra foliata* (After Maheshwari ) A–A single megaspore mother cell; B–A megaspore mother cell undergoing meiotic division; C–A tetrad of megaspores; D—A tetranucleate functional megaspore.

GAMETOPHYTIC GENERATION—The microspores and the megaspores represent the earliest stages of the male and the female gametophytes.

**Male gametophyte**—The microspore nucleus, soon after its formation inside the microsporangium, undergoes four successive divisions. Two prothallial cells (one of which is not demarcated by a wall) are formed by two successive divisions (~~fig. 9-5 A & B)~~. The antheridial initial, as a result of the third division, forms a tube nucleus and a generative or antheridial nucleus (~~fig. 9-5 C &~~ D). The latter divides again to form a sterile cell nucleus and a spermatogenous cell nucleus (~~fig. 9-5 E & F~~). The microspores are now shed from the microsporangium at this 5-nucleate stage (fig. 9-5 F) whereas, microspores of *Welwitschia* and *Gnetum* are shed at 3-nucleate stage.

According to the observations of Maheshwari[1], the male strobilus in *E. foliata* at Agra appeared in the first week of January and the shedding of pollen started from the second week of February and continued till the end of March. The flowering and fruiting periods may sometimes vary with the variations of the climate.

**Female gametophyte**—With the initiation of the development of female gametophyte, the megaspore undergoes free nuclear divisions. Land[2] counted nearly 256 nuclei in *E. trifurca* while Maheshwari[1]

1. Maheshwari, P. 1935.
2. Land, W. J. C. 1904.

observed about 500 nuclei in *E. foliata* before the walls were laid down. As a result of cell wall formation the female gametophyte becomes cellular, the lower zone forms the food storage tissue while in the upper micropylar zone develop the archegonia (fig. 9-6 C). The number of archegonia varies from 1 to 3 (3 in *E. foliata* and 2 or 1 in *E. trifurca*). Each archegonium is formed from a single superficial cell at the micropylar end of the female gametophyte as in the conifers. The archegonial initial, as a result of periclinal division, forms an outer primary neck cell and an inner central cell. The primary neck cell divides to form a long neck, 30 to 40 cells in height (fig. 9-6 C). The divisions in the beginning are regular and hence the cells of neck are arranged in regular tiers, but later the divisions become irregular. According to Land[1] the neck of the archegonium in *Ephedra* is the longest among the living gymnosperms. The central cell forms a ventral canal nucleus and an egg nucleus. The ventral canal nucleus sometimes degenerates soon after its formation. The cells situated around the central cell also divide and form one to two-layered archegonial jacket.

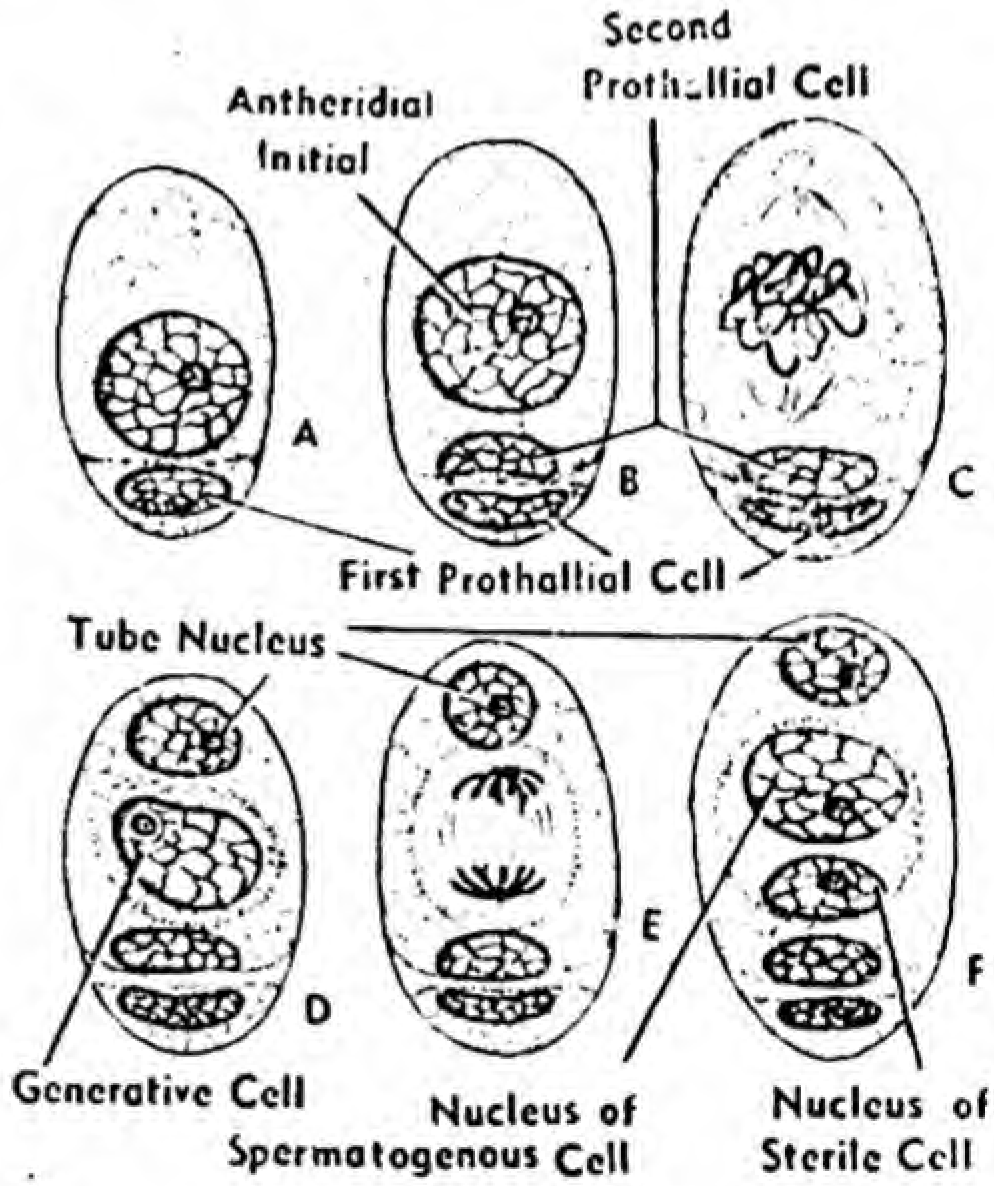



Fig. 9—5 Development of male gametophyte in *Ephedra trifurca* A—Formation of first prothallial cell; B—Formation of second prothallial cell; C—Division of antheridial initial; D—Formation of the generative cell and the tube nucleus, E—Division of generative cell; F—Formation of sterile and spermatogenous cell nuclei (After Land).

**Pollination**—As in other gymnosperms pollination in *Ephedra* is anemophilous. The pollen grains with five nuclei (fig. 9-5 F) are carried by wind to the female gametophyte. They get lodged at the micropylar aperture from where they are presumably sucked in by a pollination drop into the pollen chamber. The pollen

1. Land, W. J G. 1904.

chamber is formed by the disorganisation of the cells of the nucellus above the female gametophyte. Pollen grains germinate within a few hours of their entry into the pollen chamber. The exine ruptures and a pollen tube is formed.

**Fertilization**—The microspore germinates inside the pollen chamber. The exine ruptures and the intine elongates to form a pollen tube. Spermatogenous cell ( =body cell ) nucleus divides to form two unequal male nuclei. By this time the prothallial cells degenerate. The pollen tube pierces its way into the neck cells of the archegonium and ultimately it bursts apically. The tube nucleus, stalk cell and the two male nuclei are then released into the cytoplasm of the mature egg. Land[1] states that fertilization occurs 10 hours after pollination in *E. trifurca*. The egg at the time of fertilization is surrounded by a cytoplasmic sheath. Usually a male nucleus fuses with the egg nucleus and a zygote is formed.

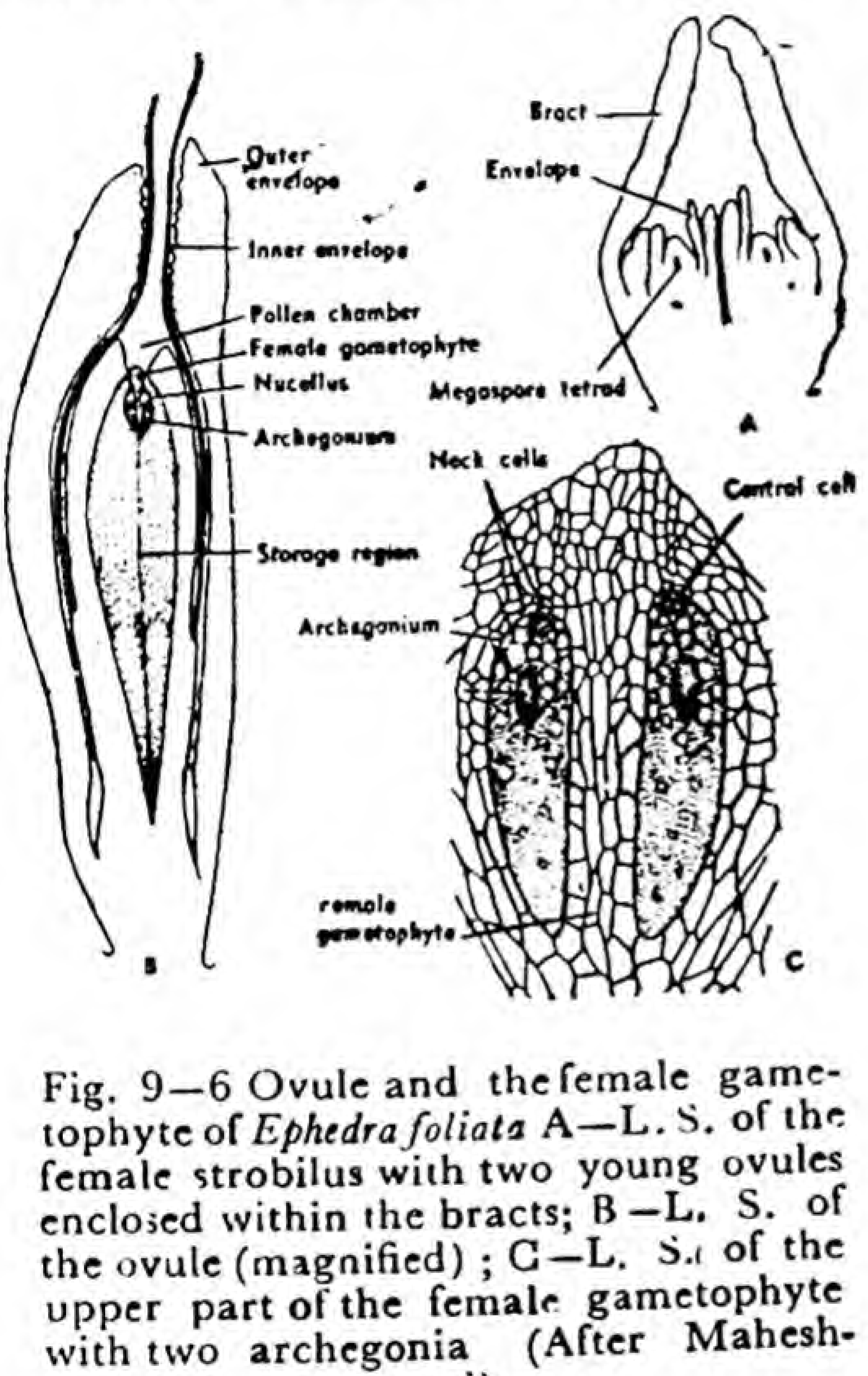



Fig. 9—6 Ovule and the female gametophyte of *Ephedra foliata* A—L. S. of the female strobilus with two young ovules enclosed within the bracts; B—L. S. of the ovule (magnified) ; C—L. S. of the upper part of the female gametophyte with two archegonia (After Maheshwari).

In *E. foliata*, Khan[2] noted that the second male nucleus may occasionally fuse with the ventral canal nucleus, but this fusion does not result in the formation of an embryo. Thus Khan[2] concluded : "The type of 'double fertilization' as seen in *Ephedra* may have no phylogenetic significance at all and may simply be a natural outcome of a tendency towards fusion between any two nuclei of opposite sexual potencies that happen to lie free in a common chamber."

1. Land, W. J. G. 1907.
2. Khan, R. 1943.

According to Maheshwari[1] the number of chromosomes in a mature egg is 7 in most of the species of *Ephedra*.

DEVELOPMENT OF THE EMBRYO—The zygote nucleus undergoes free nuclear divisions in *E. trifurca* and *E. foliata*. Such divisions end with the formation of 8 diploid nuclei which get surrounded by walls around them. This eight-celled stage is the 'proembryonal stage'. These proembryos later develop into full embryos. Hence in *Ephedra* precocious cleavage polyembryony takes place. Land[2] observed that only the cells of the lower part of proembryo ultimately develop into embryos, but Khan[3] observed that out of the 8 cells of proembryo, 6 were embryos in different stages of development (fig. 9-7 A). In *E. foliata* Khan[3] noticed that proembryonal cells develop tubular protuberances called 'suspensor tubes' (fig. 9-7 B). The nuclei of these tubes divide into two, one of which migrates to the tip of the tube, the others remaining in the middle. A transverse partition later divides the embryonal initial from the elongated suspensor cell. Secondary suspensors have also been observed in *E. trifurca*. The embryonal initial later develops into the embryo. It undergoes a transverse division forming 2 cells (fig. 9-7 C &D), the apical cell now

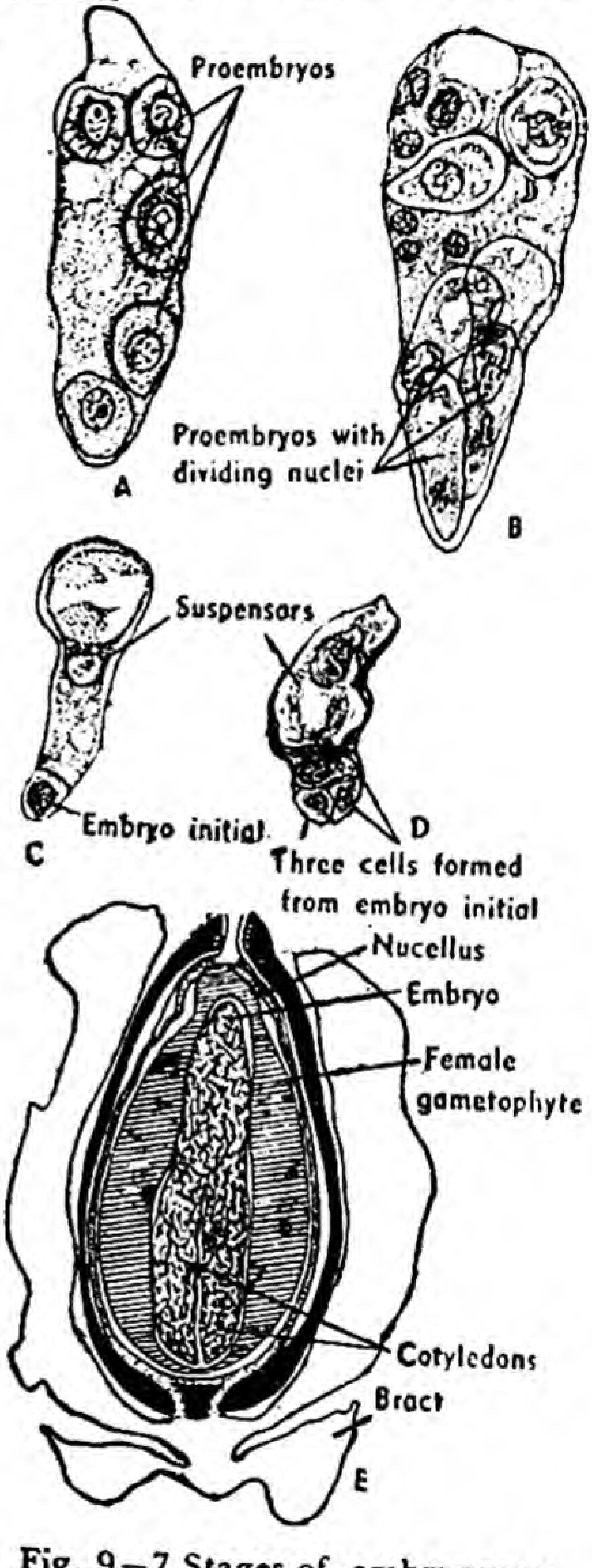



Fig. 9—7 Stages of embryogeny and the structure of seed of *Ephedra foliata* (After Khan). A—L. S. of the embryo with 5 (out of 8) proembryos; B—L. S. of the embryo with 6 proembryos in different stages of development; C & D—Dev lopment of embryo: E—L. S. of a mature seed with internal details.

1. Maheshwari, P. 1935. 2. Land, W. J. G. 1907. 3. Khan, R. 1943

divides vertically, thus three cells are formed (fig. 9-7 D). Multicellular secondary suspensor is formed from the cell next to the suspensor cell. The two cotyledons and the shoot apex develop from the lower end of the embryo. Khan[1] observed 18 to 19 embryos in different stages of development in a single ovule. He interpreted the occurrence of such a large number of embryos as the result of the combination of simple as well as cleavage polyembryony. Out of the several embryos developing in a seed, only one ultimately matures while others perish.

**Structure of the seed**—The seed of ~~*E. foliata*~~ consists of two large cotyledons which remain embedded within the tissue of the female gametophyte. There are two distinct seed coats derived from the two layers of envelope. With the development of the seed an additional thick and fleshy layer also develops round the seed; this is formed by the fusion of the subtending bracts of the strobilus. Thus a mature seed of *Ephedra* has three distinct protective coverings (fig. 9-7 E).

**Germination of the seed**—In *Ephedra* the seed is said to have no resting period. Land[2] reported that the cotyledons grow steadily until they become several centimetres long. Because of the scaly nature of leaves from the very beginning, cotyledons serve as assimilatory organs during the early stages of development of the plant. Each cotyledon possesses two parallel-running vascular bundles which are united at the base.

**~~Economic~~ importance**—*Ephedra sinica, E. gerardiana, E. nebrodensis* and also *E. intermedia* yield ephedrine used in the treatment of hay fever and asthma.

## *GNETUM* Linn.

SYSTEMATIC POSITION—

Order—*Gnetales*

Family—*Gnetaceae*

Genus—*Gnetum* Linn.

GEOGRAPHICAL DISTRIBUTION—*Gnetum* includes nearly 40 species which occur mostly in the tropical and humid regions of the earth. *Gnetum* grow in South America, in West Africa, in the Andaman and Nicobar Islands, Philippines, New Guinea, Siam, China, Burma, Pakistan, India etc. In India, *Gnetum* is represented by the following six species:

1. Khan, R. 1943.
2. Land. W. J. G. 1907.

*G. gnemon* Linn. grows in Assam, the Lushai and the Naga Hills, Golaghat area, Sibsagar, Kungaba, etc. *G. montanum* Mgf. grows in Sikkim, Assam, Sylhet, Mahrabbi, Mayurbhanj (Orissa) etc., *G. ula* Brongn grows in Western and Eastern coasts of India, near Khandala, Kanara, Coorg, Kerala, Nilgiris, Chednath Nair, Godavari District and Orissa, etc. It is a most commonly occurring species in India. *G. contractum* Mgf. grows in Kerala, the Nilgiri Hills and Coonoor, and *G. oblongum* Mgf. occurs in Bengal and Burma. *G. latifolium* Bl. var. *macropodum* Kurz occurs in the Andaman and Nicobar islands.

MORPHOLOGICAL FEATURES—The adult plant of *Gnetum* is a sporophyte resembling a dicotyledonous angiosperm in appearance. *G. neglectum* Bl. *G. latifolium* Bl. var. *funiculare* Bl. Mgf., *G. africanum* Welw, *G. ula* Brongn. are woody climbers with twining stems, while *G. gnemon* is a woody tree. In climbers generally the lower portion of the stem is devoid of leaves. In some species of *Gnetum* branches are dimorphic, i.e , they are of limited and unlimited growth, but it is not so in *G. gnemon*. Stem in several species of *Gnetum* is articulated. In climbing species foliage leaves occur on short unbranched shoots. Waterkeyn[1] noted the presence of accessory buds in *G. africanum*. The leaves of *Gnetum* resemble those of an angiosperm in reticulate venation and leathery texture (fig. 9-8 A&B). Branches arise in the axil of leaves and the stems are usually jointed. Foliage leaves are large, oval and


Fig. 9—8 Form and arrangement of leaves of *Gnetum gnemon* A—Portion of a twig with opposite and decussate leaves; B—a leaf with reticulate venation.

1. Waterkeyn, L. 1959.

entire. They are arranged in decussate pairs (fig.9-8A). Scale leaves may also be present. *G. trinerve* Spruce is said to be a parasite.

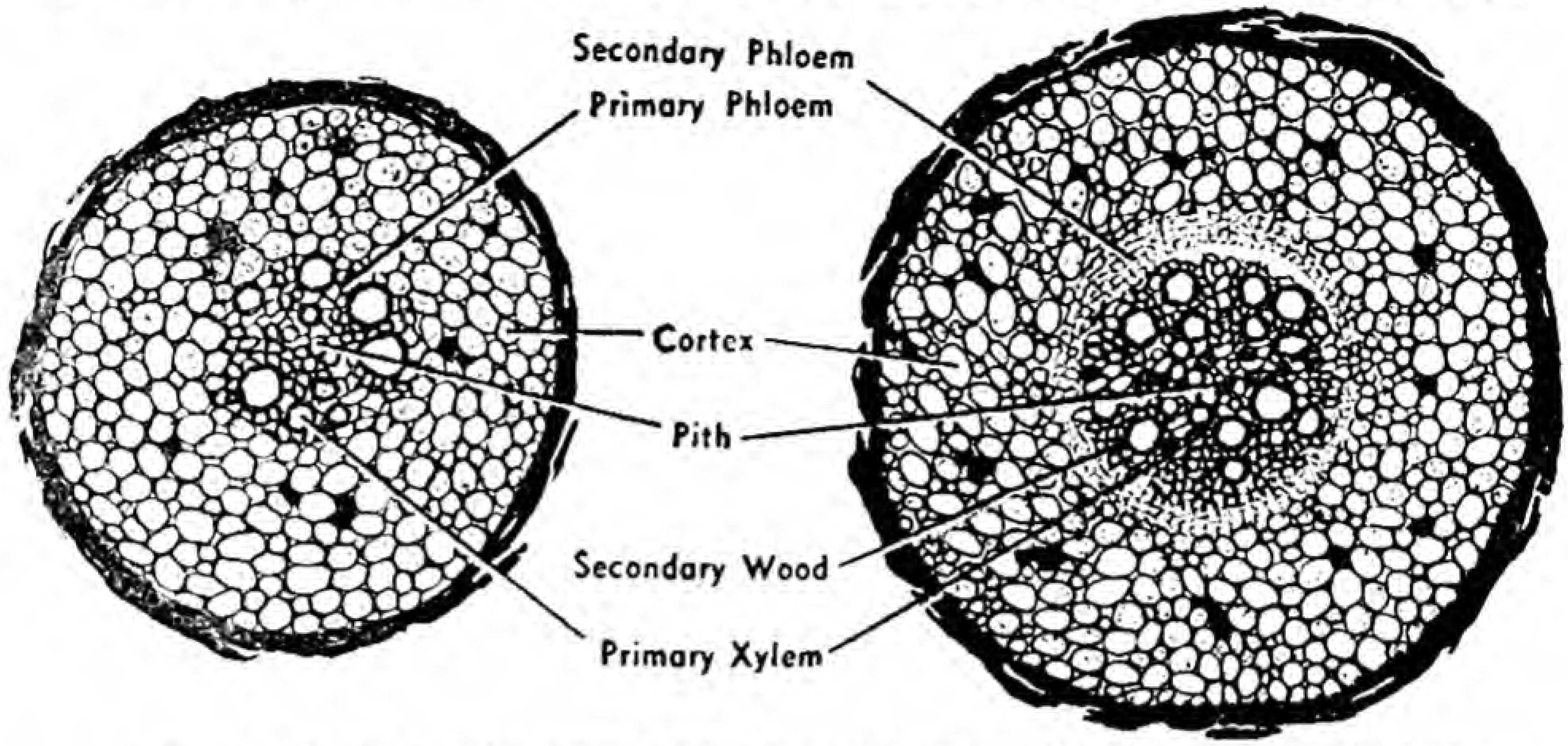



Fig. 9—9 T. S. of a young and an old root of *Gnetum gnemon* (After Maheshwari and Vasil).

HISTOLOGICAL FEATURES—The root of *Gnetum* is normally diarch, and resembles the angiosperm root in its structure and arrangement of tissues. The transverse section of a young root (fig. 9-9) reveals a multilayered parenchymatous cortex, the cells of which are oval or polygonal and full of starch grains. Thick-walled fibres are sometimes said to be present in it (fig. 9-10). There occurs a single - layered endodermis around the pericycle. Primary xylem becomes indistinct after secondary growth. Secondary growth is of normal type (fig. 9-9). Wood consists of tracheids possessing uniseriate bordered pits. Pits occurring on the vessels may be bordered or simple, small and multiseriate. Crassulae are usually absent. Phloem consists of sieve cells and parenchyma. Medullary (xylem) rays are broad but thin-walled

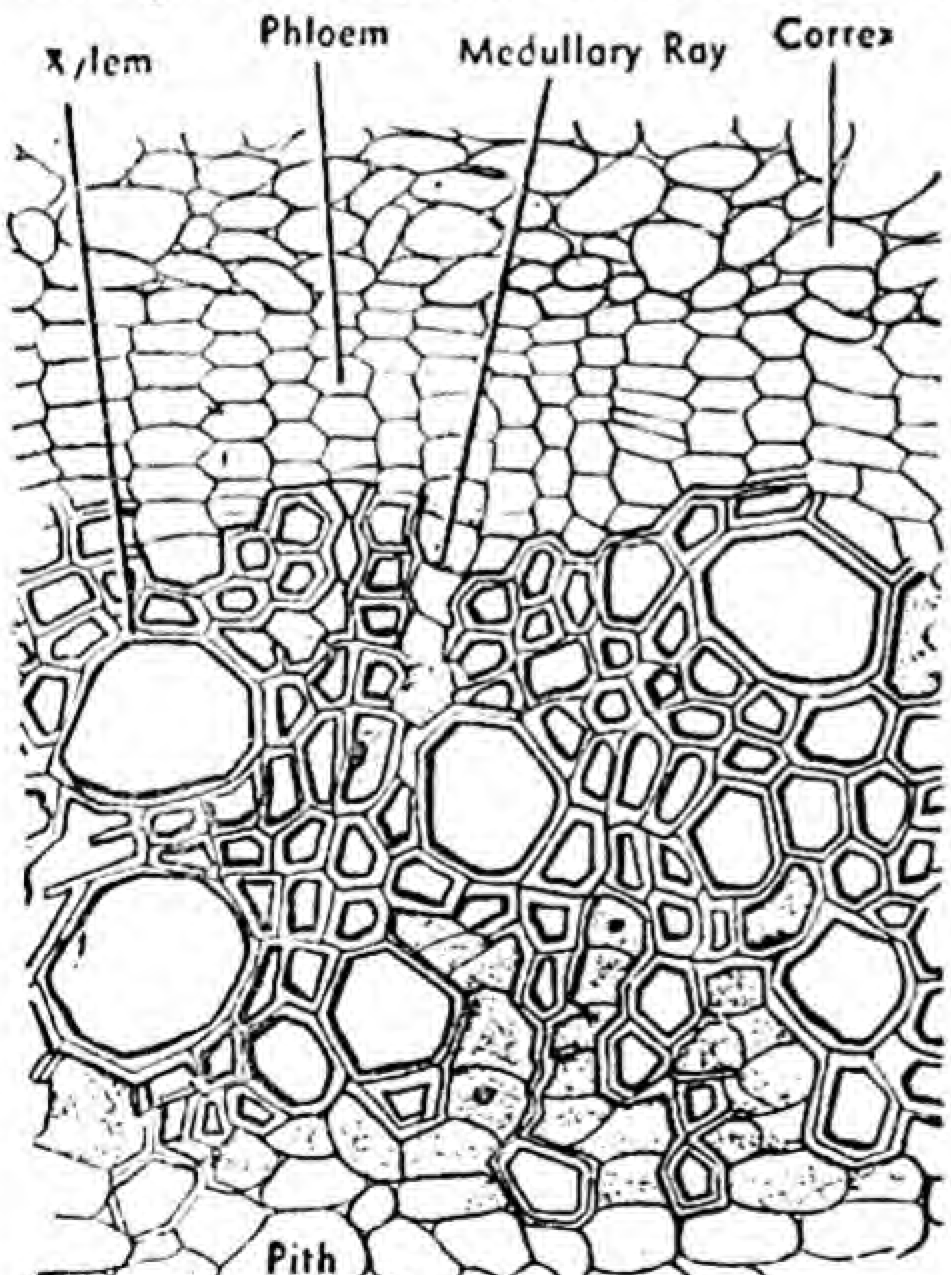



Fig. 9—10 Portion of the transection of root of *Gnetum gnemon* (After Maheshwari and Vasil).

(fig. 9-10). Diarch roots have been reported in *G. ula* and *G. gnemon.*[1]

The stem of *Gnetum*, like that of a dicotyledonous angiosperm possesses a ring of 20 to 24 conjoint, collateral and endarch vascular bundles separated from one another by broad medullary (xylem) rays (fig. 9-11). Towards outside there is a broad cortex, 12 to 16 layered thick (fig. 9-11). The stem in transverse section shows a single-layered epidermis, the cells of which are papillate and rectangular with thickened outer walls. Cuticle is thick and the

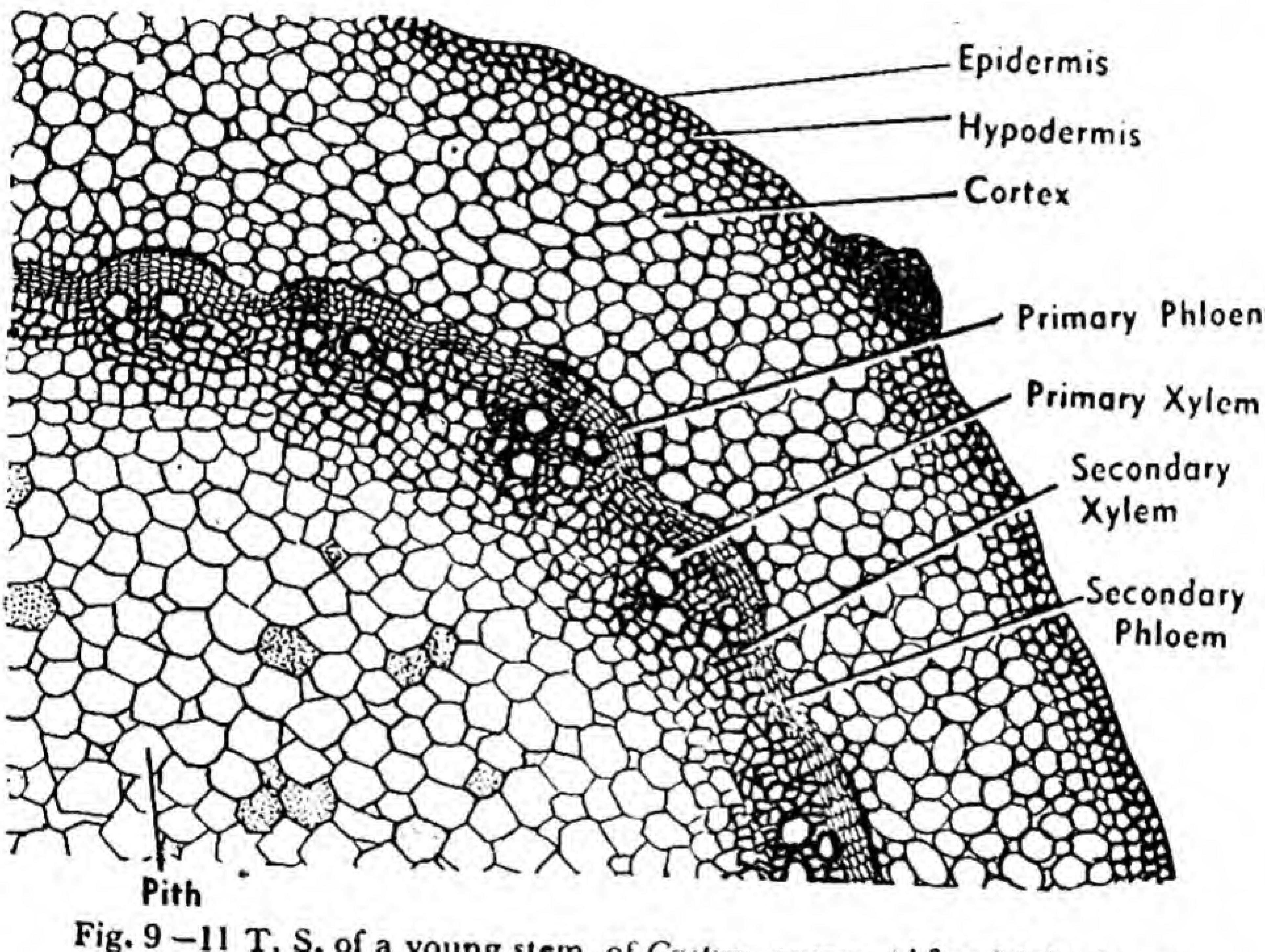



Fig. 9–11 T. S. of a young stem of *Gnetum gnemon* (After Maheshwari and Vasil).

stomata are sunken. The multi-layered cortex in older stems develops an irregular ring of sclerenchymatous tissue. Endodermis and pericycle are indistinct. Wood is mostly composed of a large number of tracheids and a few vessels (fig. 9-12). Phloem consists of sieve cells and phloem parenchyma. Pith is somewhat circular in outline and made up of parenchymatous cells which are round or polygonal in outline. In older stems a few cells of the pith may become lignified and pitted.

**Secondary growth**—In *G. gnemon* secondary growth is of normal type, i.e., it is the result of the activity of the fascicular cambia, (fig. 9-13) but in *G. ula* and *G. africanum* several succes-

1. Vasil. V. 1959.

sive rings of cambia develop one after the other in different parts of the cortex (fig. 9-13). These rings gradually become incorporated into a continuous xylem cylinder possessing wedge-shaped vascular bundles. The growth of the first ring stops at the beginning of the second one. Thus the successive rings are formed one after the other. Some of these remain incomplete and come to have eccentric position with regard to pith (fig. 9-14). Secondary phloem is composed of sieve cells and parenchyma cells. According to Thompson[1] the course of the development of companion cells in *Gnetum* and the angiosperms is different because in the former, companion cells and sieve cells develop from two different cells whereas in the latter, the sieve tubes and companion cells are formed from the same parent cell. In *G. ula* sclerenchymatous fibres occur in the phloem (fig. 9-12). Protoxylem elements possess spiral, annular or reticulate thickenings while the metaxylem elements possess bordered pits as well (fig. 9-15). The vessels of secondary xylem have simple pits on their radial walls. Transitional stages from many to one large perforation in the apices of the vessels can also be seen (fig. 9-15). Sometimes the cortex and the pith both possess laticiferous elements which usually develop from ordinary parenchymatous cells. Periderm is generally thin, it develops from the hypodermal region. It also possesses lenticels. Cork formation is irregular in *G. africanum*[2] and *G. ula*.

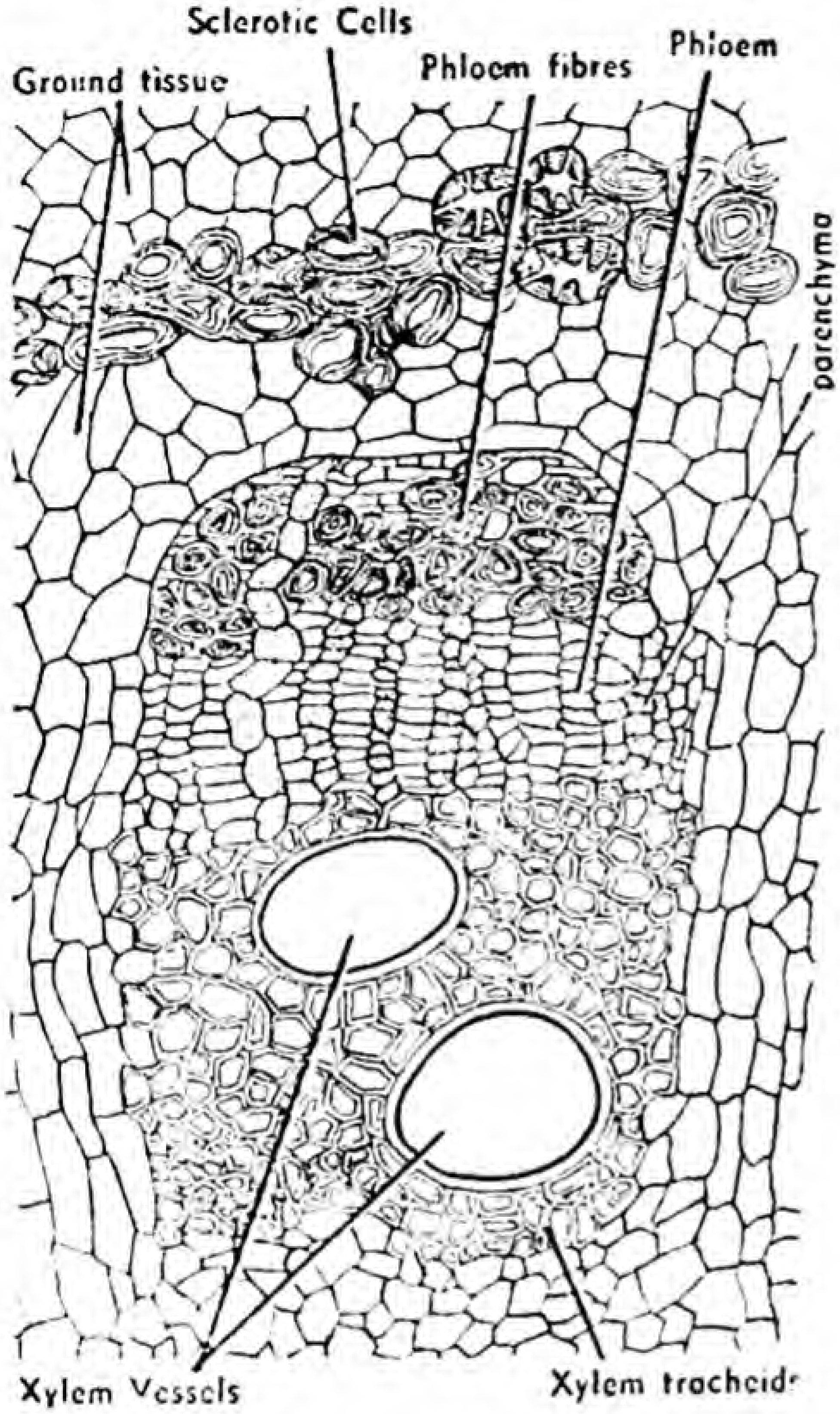


Fig. 9—12 Portion of the transection of *Gnetum ula* stem showing two xylem vessels and sclerotic cells (After Maheshwari and Vasil).

1. Thompson, W. P. 1919.
2. Duthie, A. V. 1912.

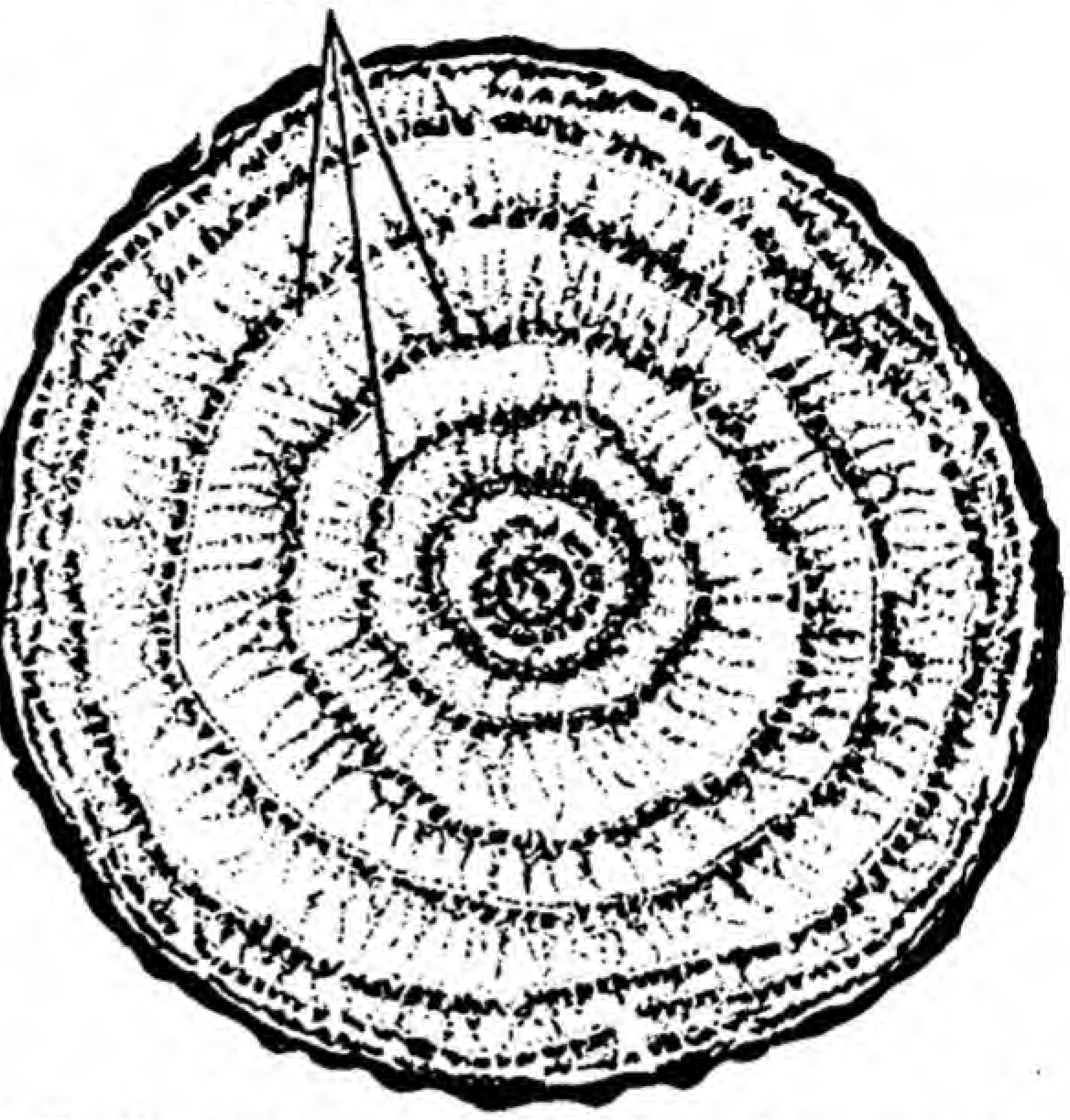



Fig. 9—13 T. S. of an old stem of *Gnetum sp.* showing vascular rings.

The leaf of *Gnetum* is apparently typically dicotyledonous, because it is dorsiventral and possesses reticulate venation in adult condition (fig. 9-8 B). The epidermis on the upper and the lower surfaces of the leaf is undulate. It possesses a well-developed cuticle on its upper side.

Stomata are mostly confined to the lower surface only. Mesophyll is differentiated into palisade and spongy tissues. Palisade tissue is usually single-cell thick. Mixed with spongy parenchyma occur branched and lignified sclerotic cells, fibres and latex tubes. Vascular bundles in the midrib region are arranged in the form of an arch followed by patches of stone cells on their lower side (fig. 9-16). Maheshwari and Vasil[1] have described that stomata in *Gnetum ula* are haplocheilic, i.e., an epidermal cell forms the stoma along with two guard cells only without the formation of subsidiary cells. In *G. gnemon* these authors report both haplocheilic and syndetocheilic development. Florin[2] on the other hand described the syndetocheilic type of stomatal development in *Gnetum gnemon*,

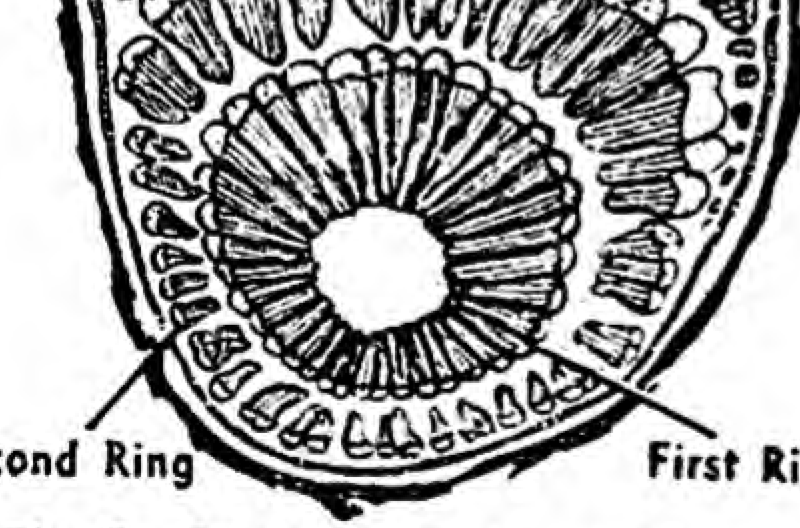



Fig. 9—14 T. S. of stem of *Gnetum ula* with eccentric secondary growth (After Maheshwari and Vasil).

1. Maheshwari, P. & V. Vasil 1961.
2. Florin, R. 1931.

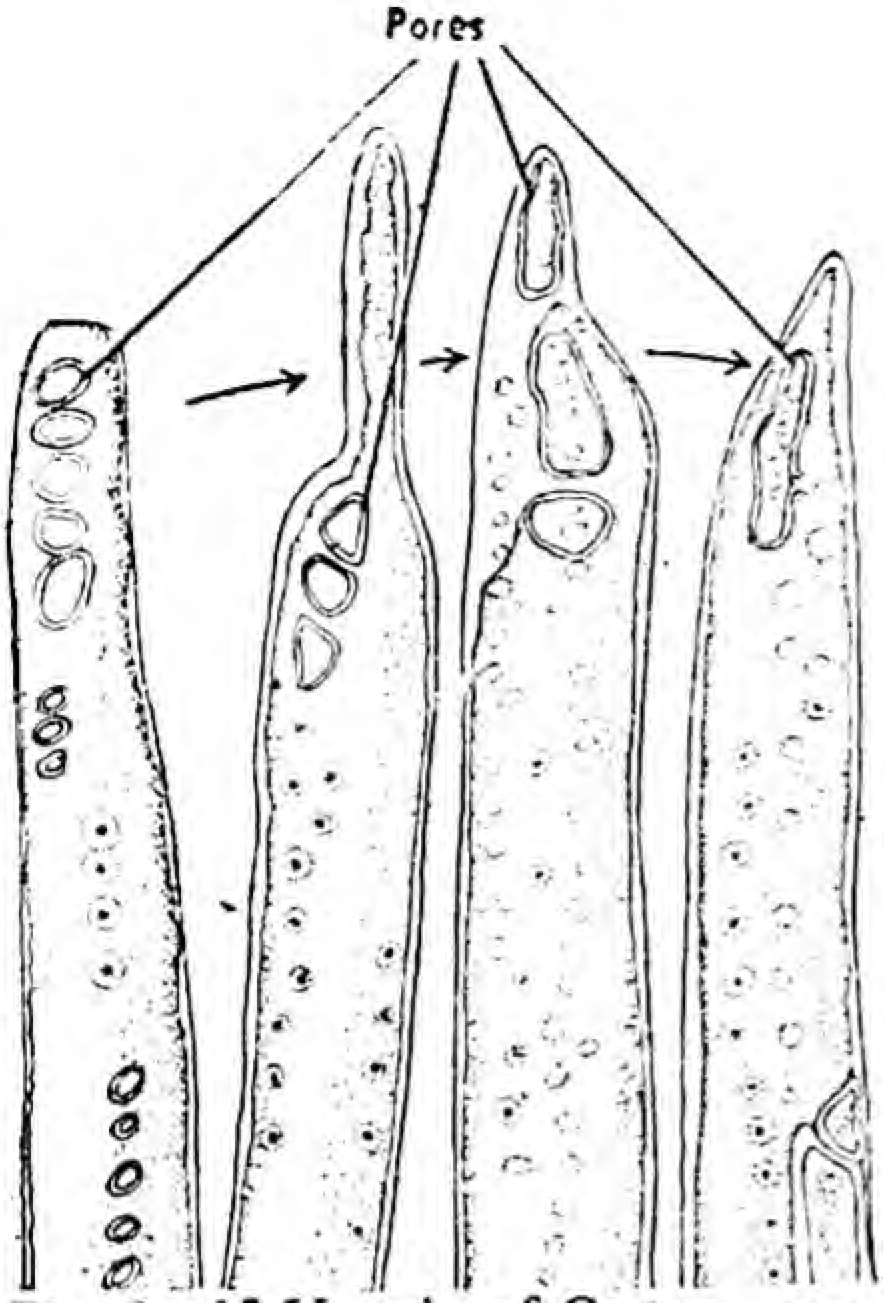



Fig. 9—15 Vessels of *Gnetum gaenon* showing the formation of a single pore from several pores. Bordered pits can also be seen (After Maheshwari and Vasil).

i. e., the epidermal cell forms the stoma along with 2 guard and 2 subsidiary cells (fig. 9-17). The development of stomata in *Gnetum* needs a critical study. Vascular bundles in the leaf are conjoint, collateral and endarch with xylem pointing towards the upper side of the leaf. Those of the petiole are associated with transfusion tissue.[1]

## LIFE-HISTORY

All the species of *Gnetum* are dioecious. Male and female strobili are organised like an inflorescence (fig. 9-18A & 9-20A) which is usually solitary and axillary but it may rarely be terminal. Strobili are rarely branched (fig. 9-18F). The strobili, whether male or female, possess a short and stout axis.

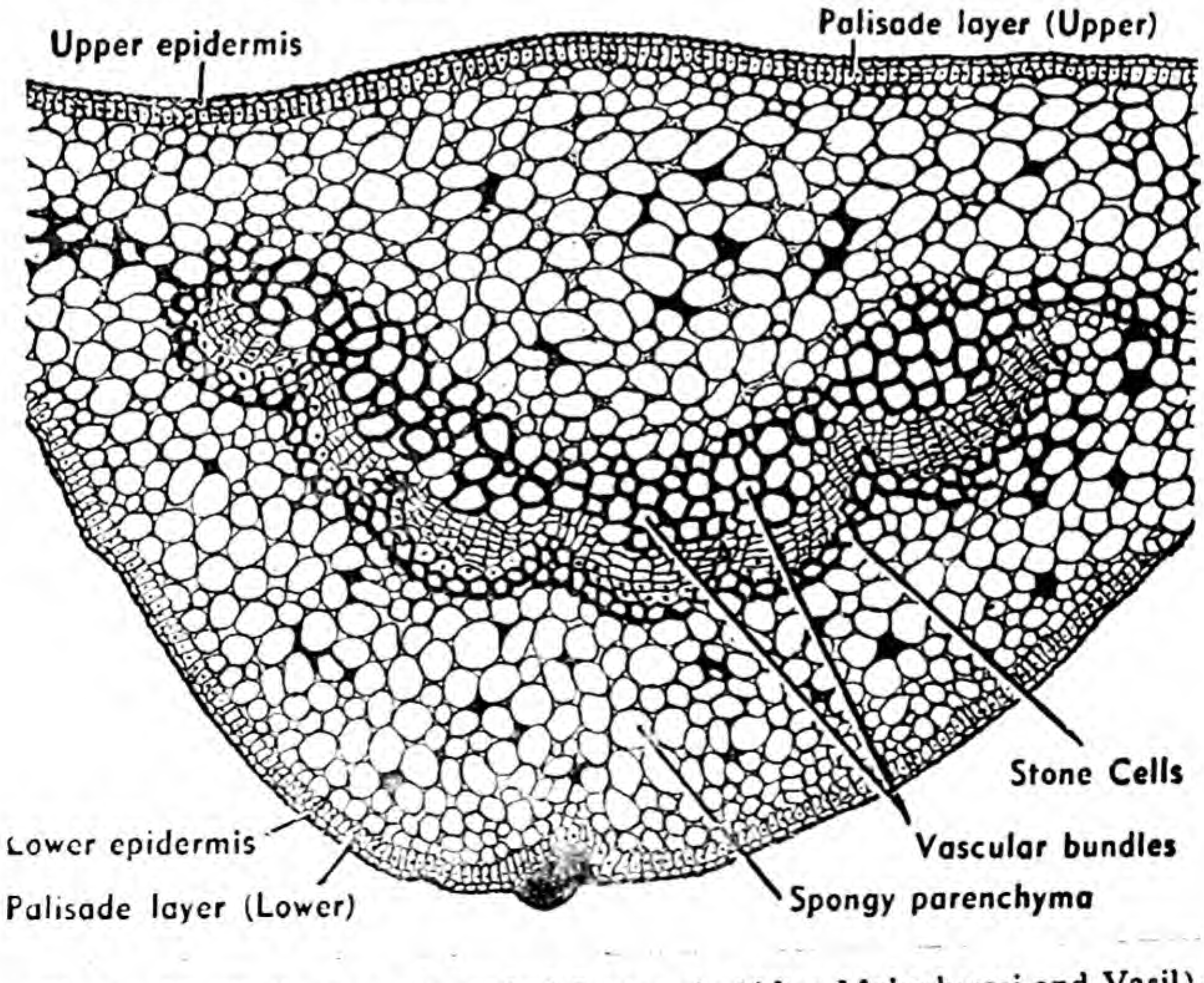



Fig. 9—16 T. S. of an old leaf of *Gnetum ula* (After Maheshwari and Vasil).

1. Rodin, R.J 1966.

In the axils of connate bracts arise the strobili. The bracts situated above the base of strobilus are arranged in a whorl, all of these fuse to form a cupule-like structure commonly called as 'collar'[1]. Each strobilus possesses 10 to 25 collars (fig. 9-18 B & F). Exceptionally the male and the female organs may be present on the same strobilus (fig. 9-18 F). In *G. africanum* rarely the female flowers occur mixed with the male but in *G. buchholzianum* Engler these occur separately.

**Male strobili (cones)**—The axis of each male strobilus possesses 10 to 15 collars. The collars are arranged one above the other (fig. 9-18 A-F). Each collar possesses 3 to 6 male flowers which are arranged in definite rings (fig. 9-18E). In young condition the male strobilus is completely enclosed by basal bracts (fig. 9-18 A & 9-20 B) but at maturity it emerges out of the collar rings (fig. 9-18E).

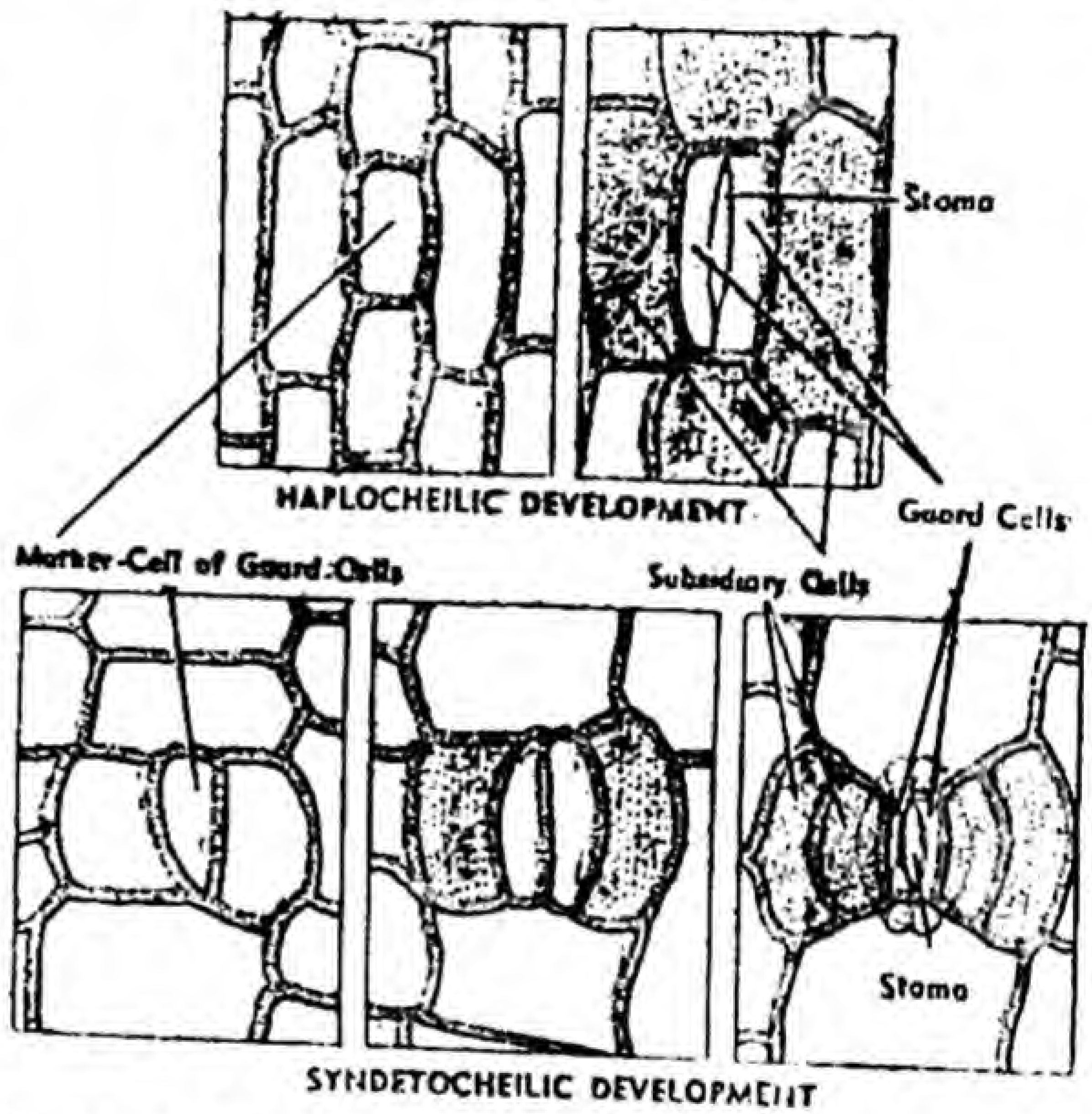



Fig. 9—17 Types of stomatal development (After Foster). Note the formation of subsidiary as well as guard cells in the syndetocheilic and only guard cells from a parent cell in the haplocheilic type of stomatal development.

**Male flowers**—Each male flower in young stage is enclosed within a sheath-like perianth. It consists of a stalk which at its apex usually bears two unilocular anthers or microsporangia (fig. 9-19 A-C). When mature the stalks elongate and push the anthers beyond the collars through a slit which is formed in the perianth (fig. 9-19 D & E). Vasil[1] and Madhulata[2] have noticed the occurrence of a single anther in *G. ula* and *G. gnemon* respectively but such occurrences are rare. Sometimes more than two anthers have also been observed in a few flowers of *G. ula* and *G. gnemon*. The anthers may seldom be fused. Young microsporangia are enclosed within

1. Vasil, V, 1959.
2. Madhulata 1960 [in Maheshwari, P. & V. Vasil 1961].

the anthers. The pollen mother-cells divide meiotically or reductionally and ultimately form the pollen grains (fig. 9-22 J-O).

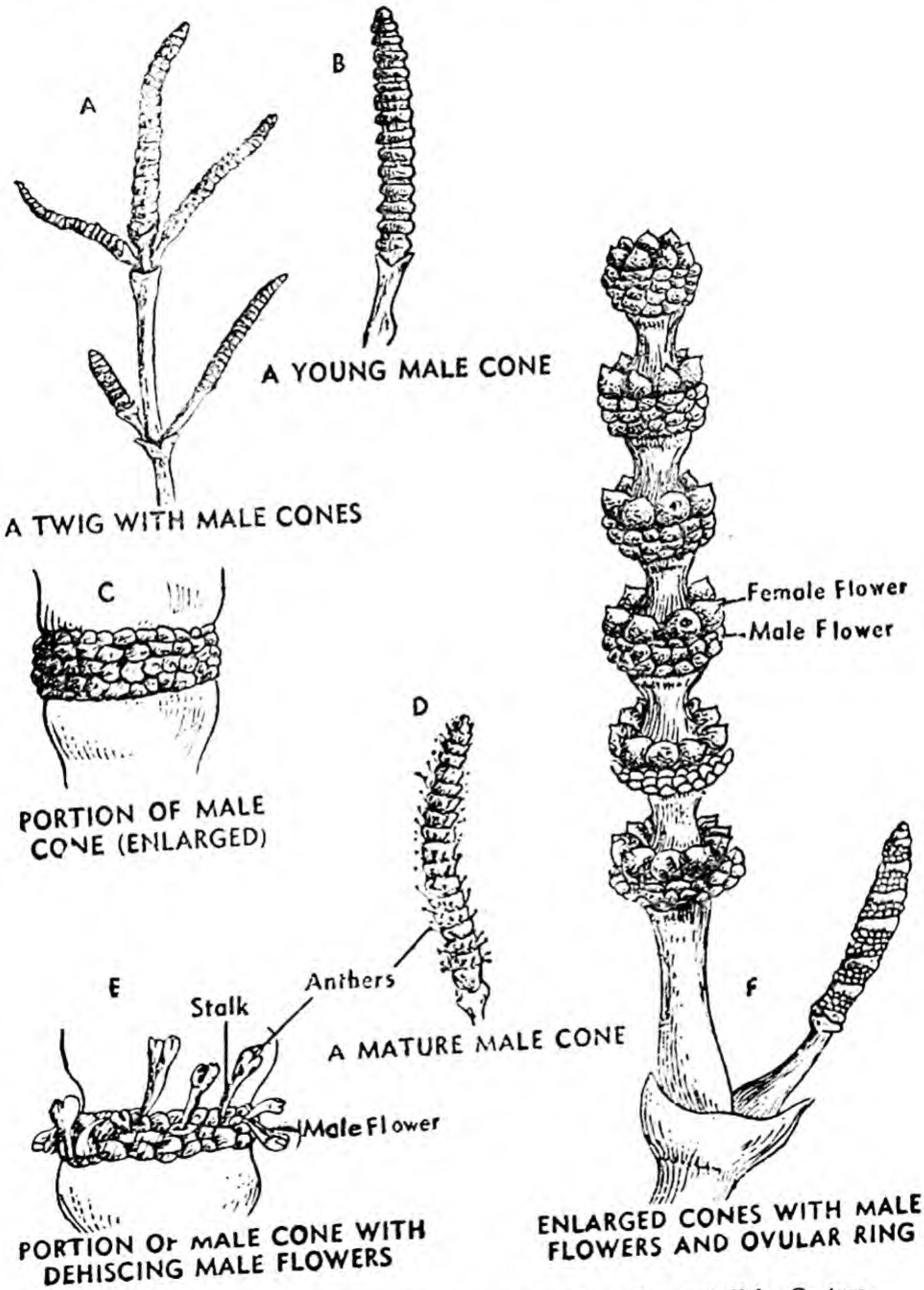



Fig. 9—18 Structure and development of male strobili in *Gnetum*. A to E—of *G. ula* (After Vasil) ; F—of *G. gnemon* with both male and female flowers (After Madhulata).

**Female strobili (cones)**—Like the male strobilus the female strobilus also possesses an axis or stalk which has collars arranged one above the other (fig. 9-20 A). Each collar bears a single whorl of 4 to 10 reduced female flowers or ovules which appear

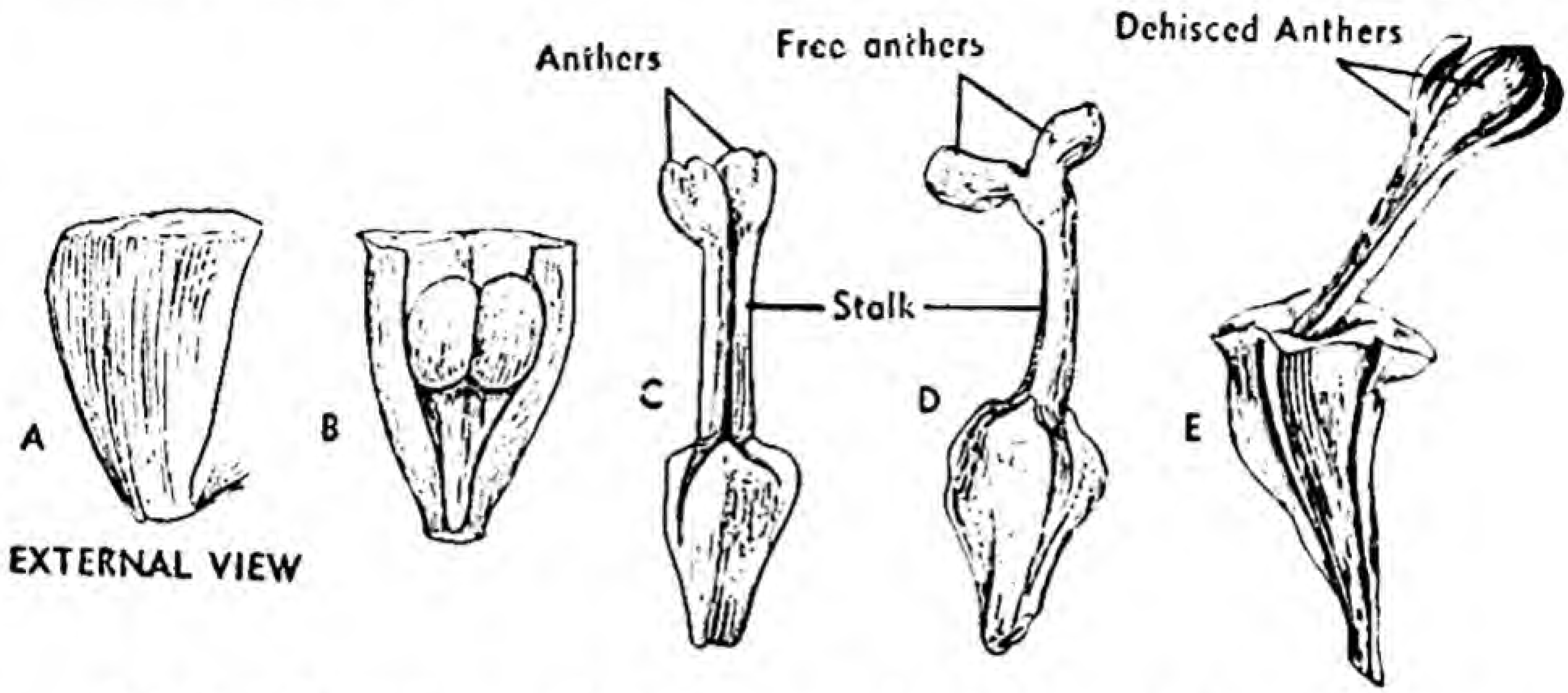



Fig. 9—19 Structure and development of male flowers of *Gnetum* A, B and E—of *G. ula* (After Vasil) ; C and D—of *G. gnemon* (After Madhulata).

as minute protuberances (fig. 9-20 B to D). Most of these do not develop further but a few ultimately mature and form seeds.

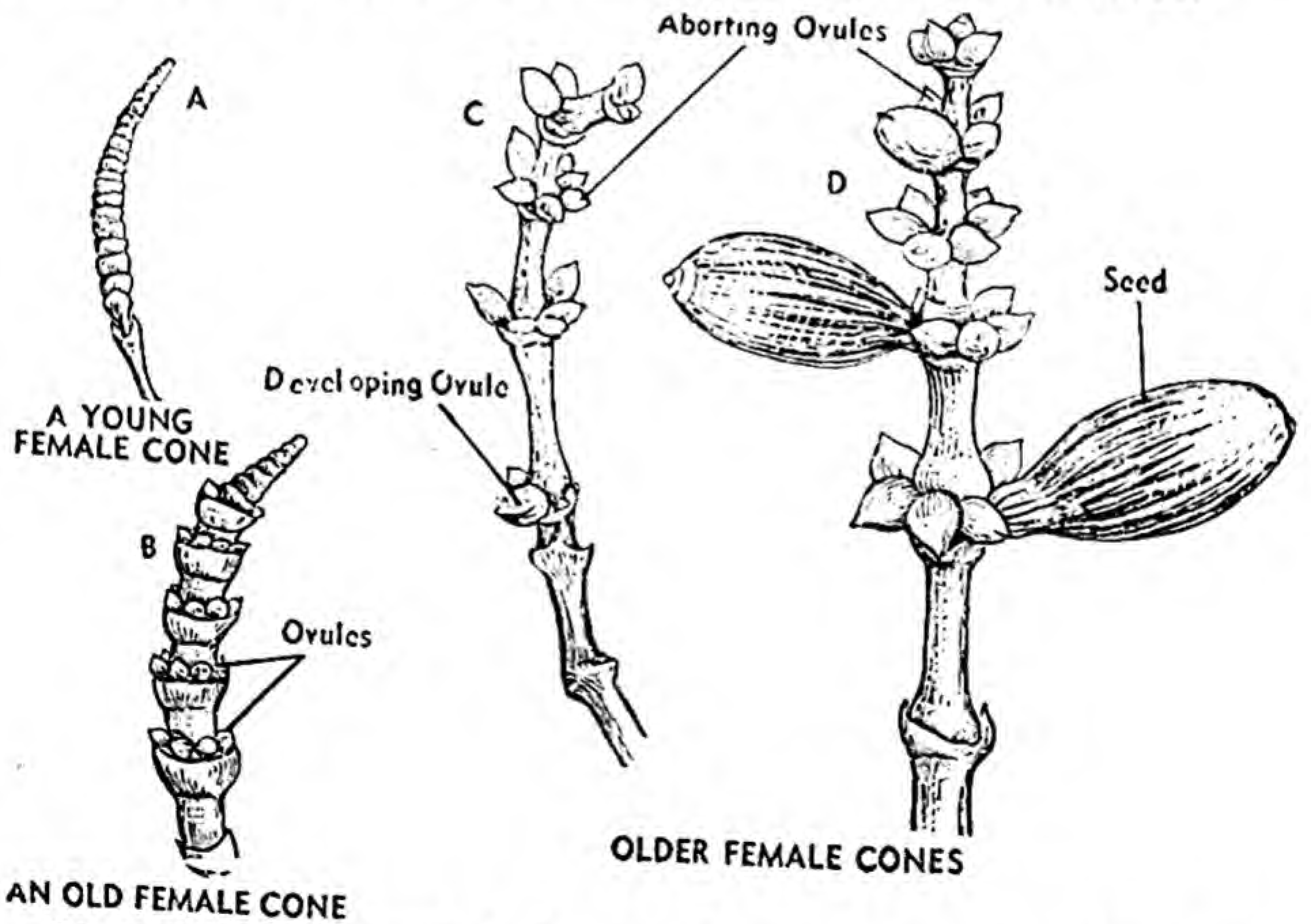



Fig. 9—20 Structure and development of the female strobili and seeds of *Gnetum* A—C of *G. ula* (After Vasil), D—of *G. gnemon* (After Madhulata).

**Female flowers**—The female flower or ovule is usually stalked, (fig. 9-20 A & B) it may rarely be sessile. Each ovule consists of

nucellus (fig. 9-23 A to D) and is surrounded by a three-layered envelope. The outermost layer of the envelope is called the perianth. The middle layer has usually been referred to as 'outer integument' and the inner one has been called the 'inner integument'. The innermost layer of the envelope gets prolonged above the ovule to form a long micropylar canal or the so-called 'style' (fig. 9-21). Exceptionally in *G. ula* a fourth layer of the envelope may be present (Madhulata[1]).

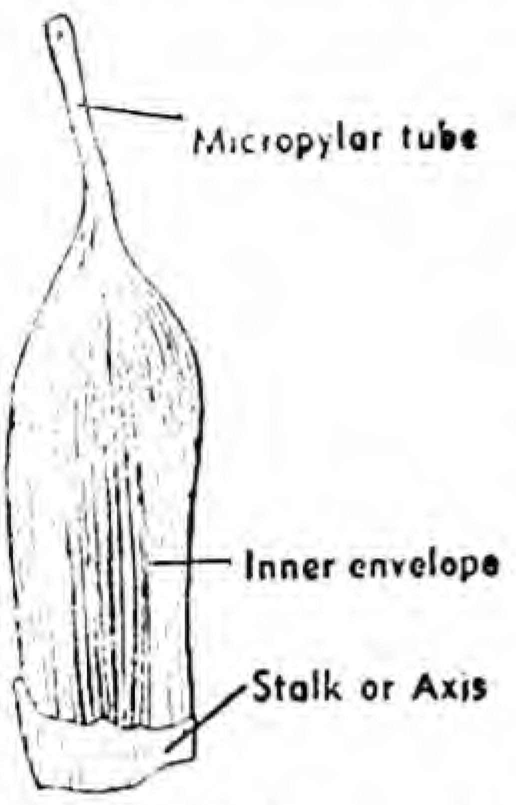


Fig. 9–21 Structure of the ovule of *Gnetum ula* after the removal of the two outer layers of the envelope (After Vasil).

**Abnormal strobili**—Thompson[2], Pearson[3], Maheshwari[4], Vasil and Madhulata[1] have reported a few abnormalities in different strobili of *G. gnemon* and *G. ula*, some of these are listed below :

There may occur a double ring of ovules in male strobili[1 & 4]. The collars may be spirally arranged in the female and male strobili[1, 2 & 5]. Sterile collars at the base may be present in the male strobili only[3]. The number of male flowers may be reduced in different strobili[1 & 3]. The ovules in the lower collars may sometimes be replaced by short male strobili[1 & 3].

In both the male and the female strobili the flowers are separated from one another by uniseriate hairs. Negi[6] observed that the hairs develop from the outermost layer of meristematic cells situated in between the ovular primordia. During megasporogenesis the hairs get shrivelled and are shed after free nuclear divisions within the female gametophyte. Biseriate hairs are very uncommon, the apical cells of these hairs rarely assume a bulbous shape.

**Sclereids and laticiferous tubes**—Branched or unbranched star-shaped sclereids possessing narrow lumen and thickened walls

1. Madhulata 1960 [Maheshwari, P. & V. Vasil 1961].
2. Thompson, W. P. 1916.
3. Pearson, H. H. W. 1912, 1915.
4. Maheshwari, P. 1953.
5. Vasil V. 1959.
6. Negi, V. 1958 [Maheshwari P. and V. Vasil 1961].

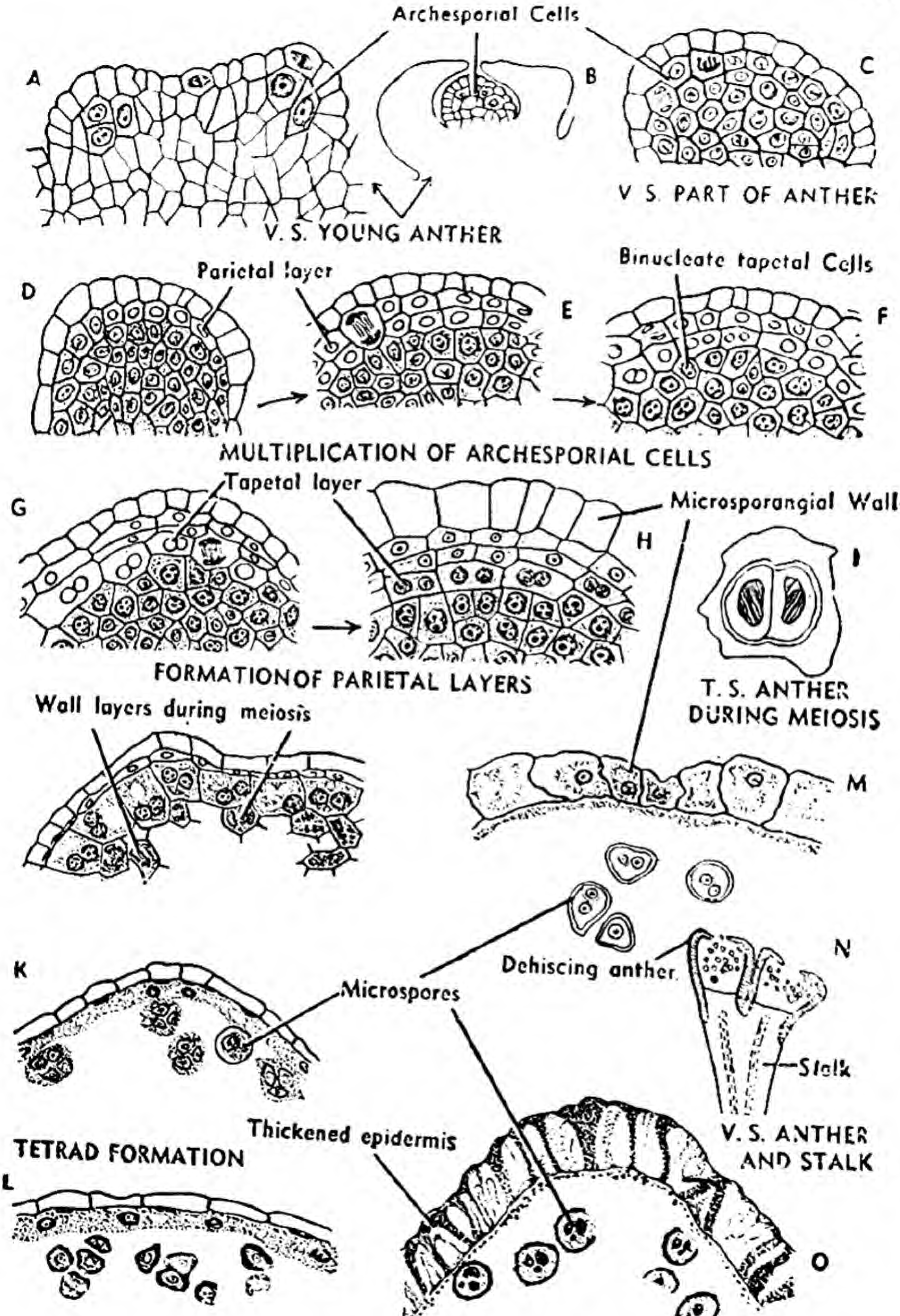



Fig. 9—22 Development of microsporangia and dehiscence of anthers in *Gnetum* A—H—Development of archesporial cells [A and H of *G. gnemon* (After Madhulata) ; B—G of *G. ula* (After Vasil)] ; I—O—Structure of anther and release of pollen grains in *G. ula* (After Vasil).

occur in the collars, perianth and stalks of male and female flowers, etc. These organs in addition to sclereids have laticiferous tubes as well[1].

**Morphological nature of the ovular envelope**—The morphological nature of the ovular envelope has been a controversial subject. Strasburger[2] thought that the 3 layers of envelope are formed by the splitting up of a single integument. Beccari[3] suggested that the two inner layers of the envelope represented the two integuments like those of an angiospermous ovule and the outermost represented the perianth. Van Tieghem[4] contended that the outer layer of the envelope was equivalent to an ovary or an organ analogous to it and the inner two layers represented the two integuments. Thompson[5] was of the opinion that the outer two layers of envelope form the perianth and the inner one is akin to angiospermous ovary. The presence of an exceptional fourth envelope in *G. ula* raises doubt about the exact morphological interpretation of these structures. It is difficult to assume two ovaries one inside the other.

**Microsporogenesis**—In young microsporangia two or more hypodermal cells become prominent (fig. 9-22 A & B). These divide further to form a multicelled archesporium (fig. 9-22 C to G). Periclinal divisions demarcate a parietal layer which surrounds the centrally situated primary sporogenous tissue (fig. 9-22 E to H). Tapetum is later cut off from the parietal layer (fig. 9-22 D & E). The sporogenous cells divide further to form the microspore mother cells (fig. 9-22 H to J).

**Megasporogenesis**—At the apex of the nucellus of the ovule occurs a small cavity, a rudimentary pollen chamber. Nucellar beak is absent in *Gnetum*. At the time of the development of the innermost layer of envelope 2 to 4 archesporial initials have already differentiated in the hypodermal region of the nucellus (fig. 9-23 A-C). These initials cut off primary parietal cells and sporogenous cells. Primary parietal cells and nucellar

1. Negi, V. 1958 [in Maheshwari, P. & V. Vasil 1961)
2. Strasburger, E 1872.
3. Beccari, O. 1877.
4. Van Tieghem, 1869.
5. Thompson, W. P. 1916.

epidermis divide repeatedly to form a massive nucellus. The sporogenous cells function as spore mother cells and arrange themselves in linear rows of 8 to 16 cells in *G. gnemon.*

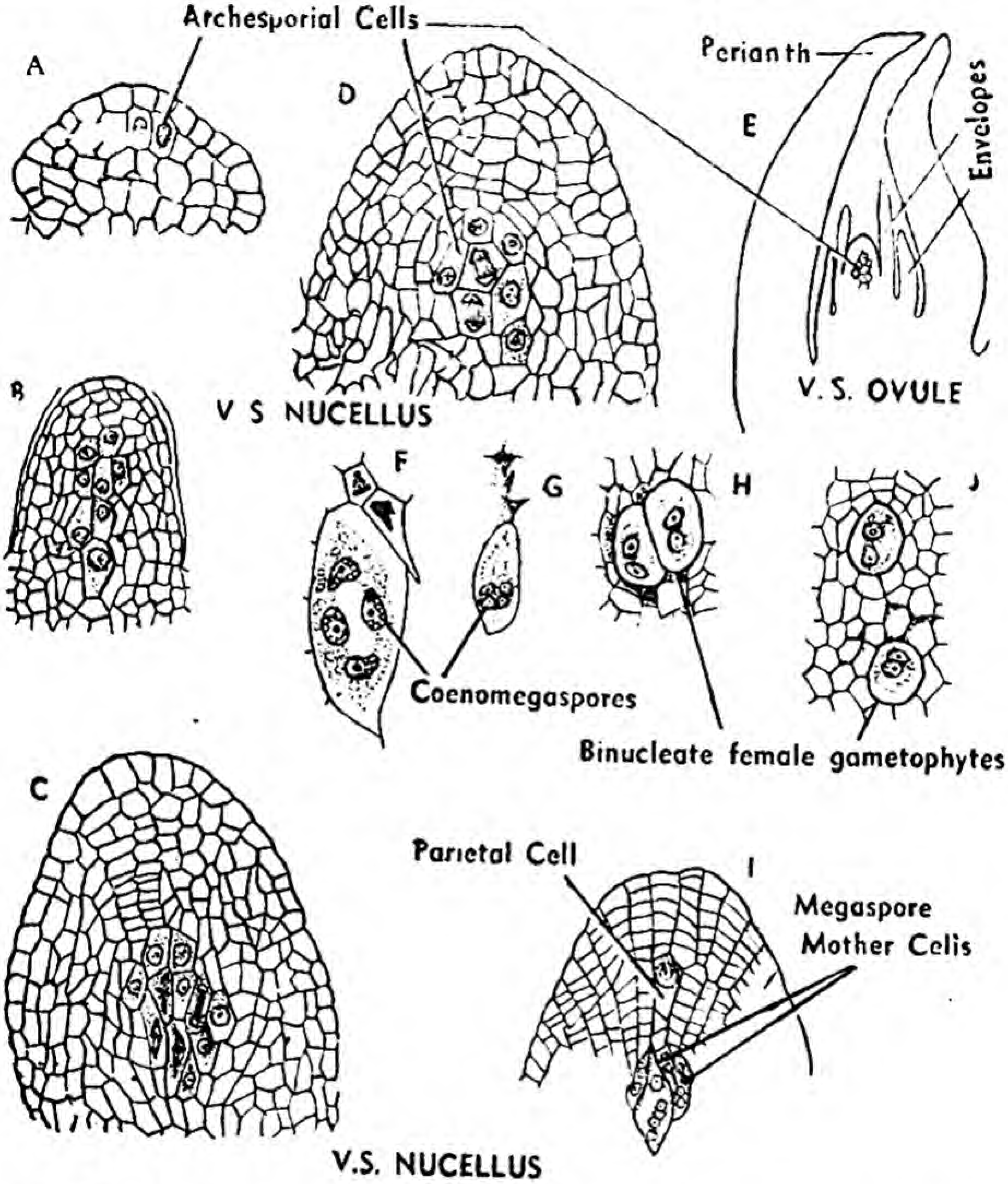



Fig. 9—23 Formation of megaspore mother cells and coenomegaspores in *Gnetum*. A—D. of *G. ula* (After Vasil) ; E and F. of *G. gnemon* (After Madhulata); G, H and J of *G. ula* (After Vasil) ; I of *G. gnemon* (After Fagerlind). Figures F and G show two degenerating megaspore mother cells.

The contention that the sporogenous cells behave directly like the megaspore mother cells is erroneous[1]. Vasil[2] and Madhulata[3] have however observed that in exceptional cases e.g.,

1. Thompson, W. P. 1916.
2. Vasil, V. 1959.
3. Madhulata 1960.

*G. ula* and *G. gnemon* an archesporial cell enlarges and without further divisions function directly as megaspore mother cell. Rarely one of the parietal cells failing to divide may also function as megaspore mother cell. Recent studies made on *G. gnemon* and *G. ula* have clearly established the fact that the development of an embryo sac is obviously of tetrasporic type similar to that of the angiosperms and not of monosporic type as suggested by Apte and Kulkarni.[1]

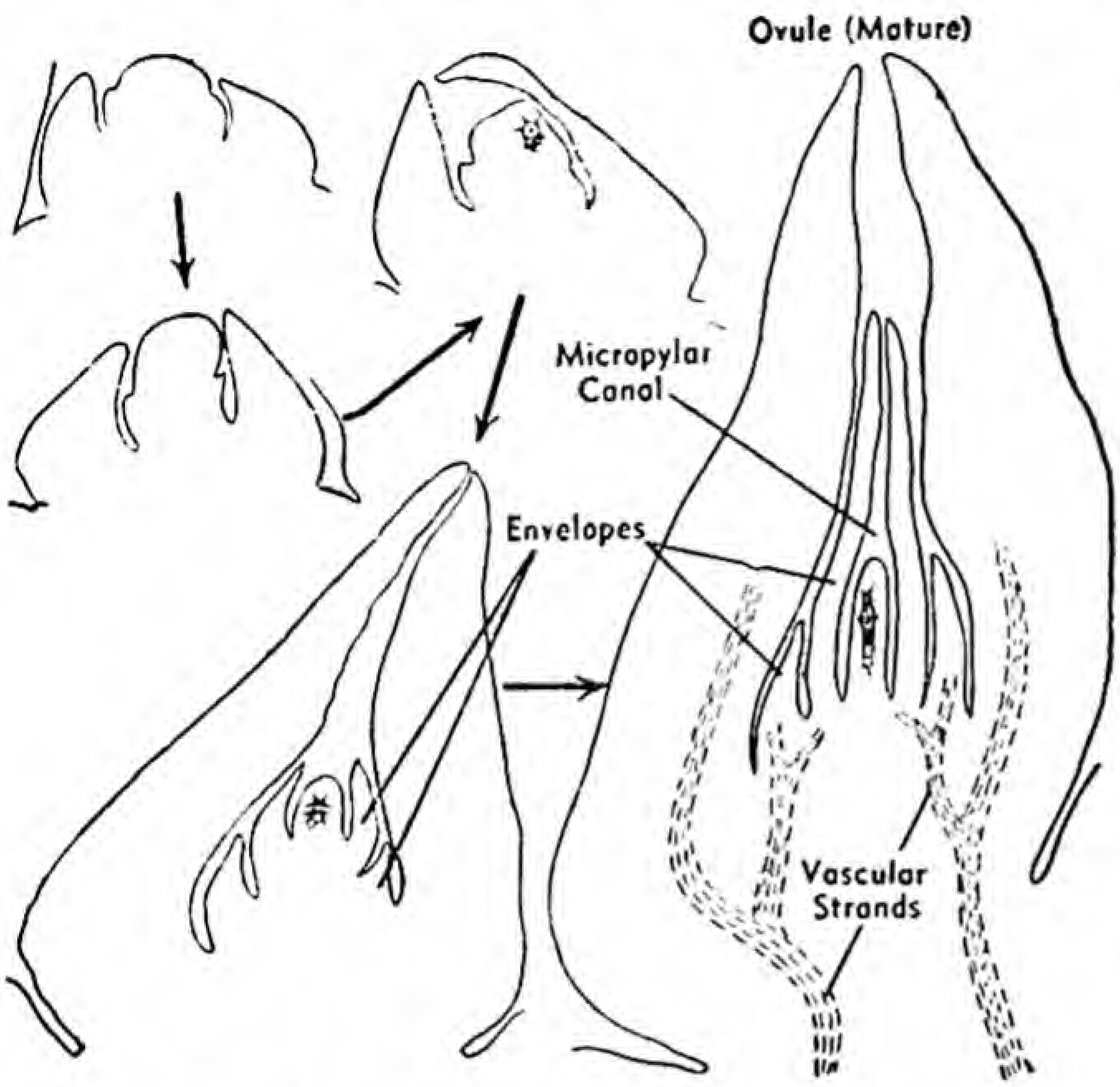


Fig. 2—24 V. S. of ovules of *Gnetum ula* showing different layers of the envelope and the micropylar canal (After Vasil).

The megaspore mother cells in general undergo a meiotic division, the two nuclei thus formed separate apart. Wall formation does not take place at this stage. Second meiotic division takes place quite late. Meanwhile most of the other developing megaspore mother cells degenerate. The two nuclei, after moving apart, move to the centre and the second meiotic division takes place at this stage which ultimately results in the formation of a tetranucleate coenomegaspore, i. e., a megaspore without any cell wall separating the nuclei (fig. 9-23F-I). Initially a large number of megaspore mother cells develop inside the nucellus but only 2 or 3 of them—by repeated nuclear divisions—reach the 16-nucleate stage while the rest degenerate.

Contrary to the opinions commonly held regarding the origin of megaspore in *G. gnemon* and *G. ula* etc., a megaspore tetrad is never formed. What appear to be like the degenerating megaspores are really the megaspore mother cells (fig. 9-23 H-I). This gives an appearance of a tetrad. In its tetrasporic nature of the female gametophyte *Gnetum* is the only gymnosperm which resembles the angiosperms. Exceptionally binucleate female gametophytes can also be seen (fig. 9-23 H-I).

1. Apte, V. V. & L. H. Kulkarni 1953.

GAMETOPHYTIC GENERATION—In Indian species of *Gnetum* the development and structure of the male gametophyte

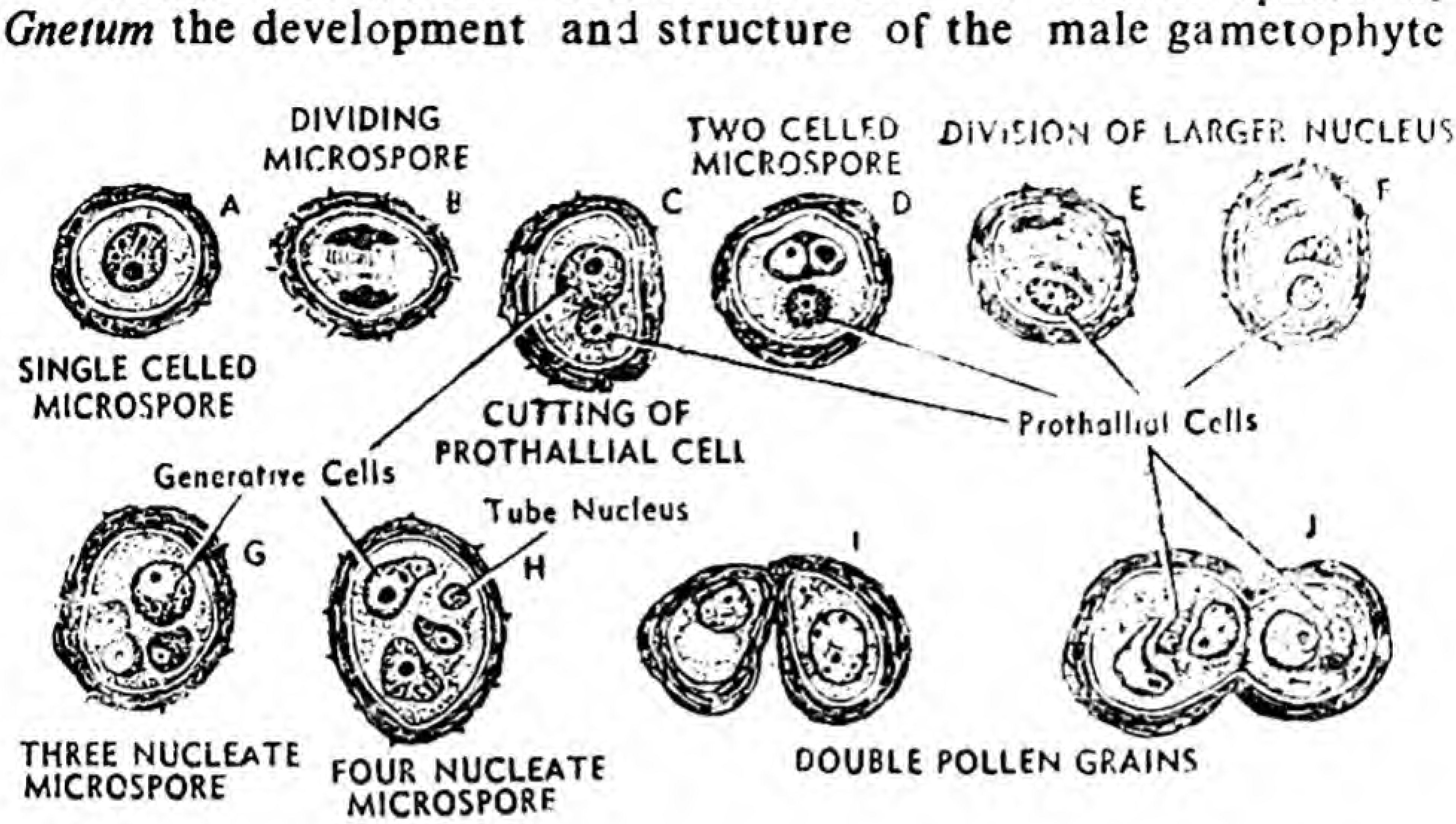



Fig. 9—25 Development of male gametophyte in *Gnetum ula*. Figures I and J show double pollen grains (After Vasil).

has been studied by Negi and Madhulata[1]. As a result of the meiotic or reduction divisions of the microspore mother cells the

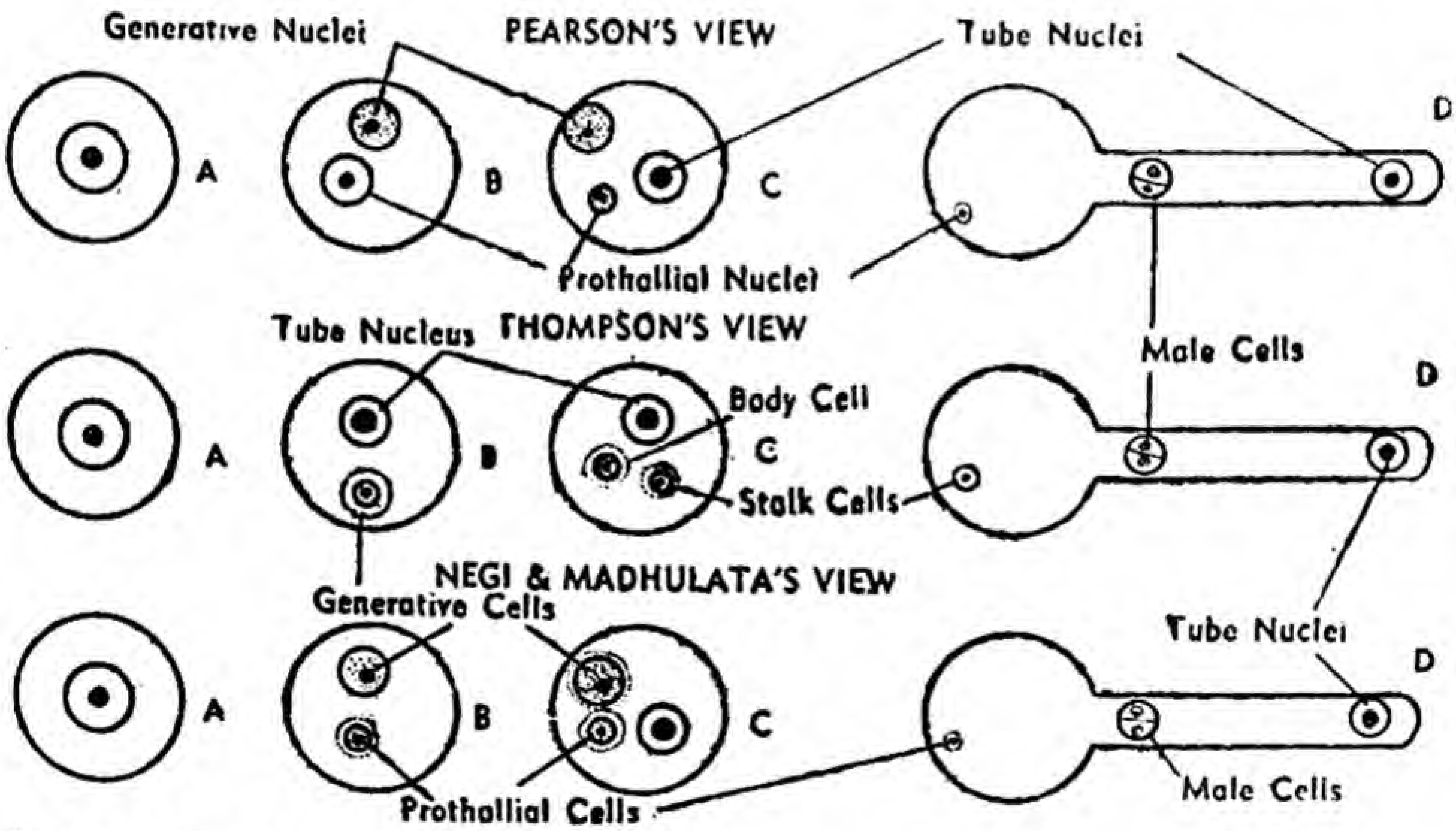



Fig. 9—26 Diagrammatic representations of the old as well as recent views on the development of the male gametophyte in *Gnetum* (After Negi and Madhulata).

microspores or pollen grains are formed in tetrads (fig. 9-22 K & L) inside the anther or microsporangium.

1. Negi, V. and Madhulata 1957.

**Male gametophyte** – Each pollen grain possesses a thick outer wall, the exine, and an inner thin layer, the intine. Pollen grain or microspore nucleus divides to form a small prothallial cell and another cell which is larger (fig. 9-25 B & C). The nucleus of the larger cell divides further into two daughter nuclei, one of them without a wall is called the tube nucleus and the other having a distinct wall is the generative cell (fig. 9-25 D-G). Pollen grains are single but there may exceptionally be double pollen grains also (fig. 9-25 I & J). Pollination takes place at the three-celled stage when the pollen grain has a small prothallial cell, a tube nucleus and a generative cell (fig. 9-25 G). Rarely, 4-celled pollen grains have also been observed (fig. 9-25 H) at the time of pollination. Pollen grains after being carried by wind reach the micropyle where they get caught in the pollination drop (fig. 9-27 A&B). After being sucked in, the pollen grains reach the rudimentary pollen chamber—a typical gymnospermous method of pollination. Pijl[1] noticed entomophilous type of pollination in *G. gnemon*.

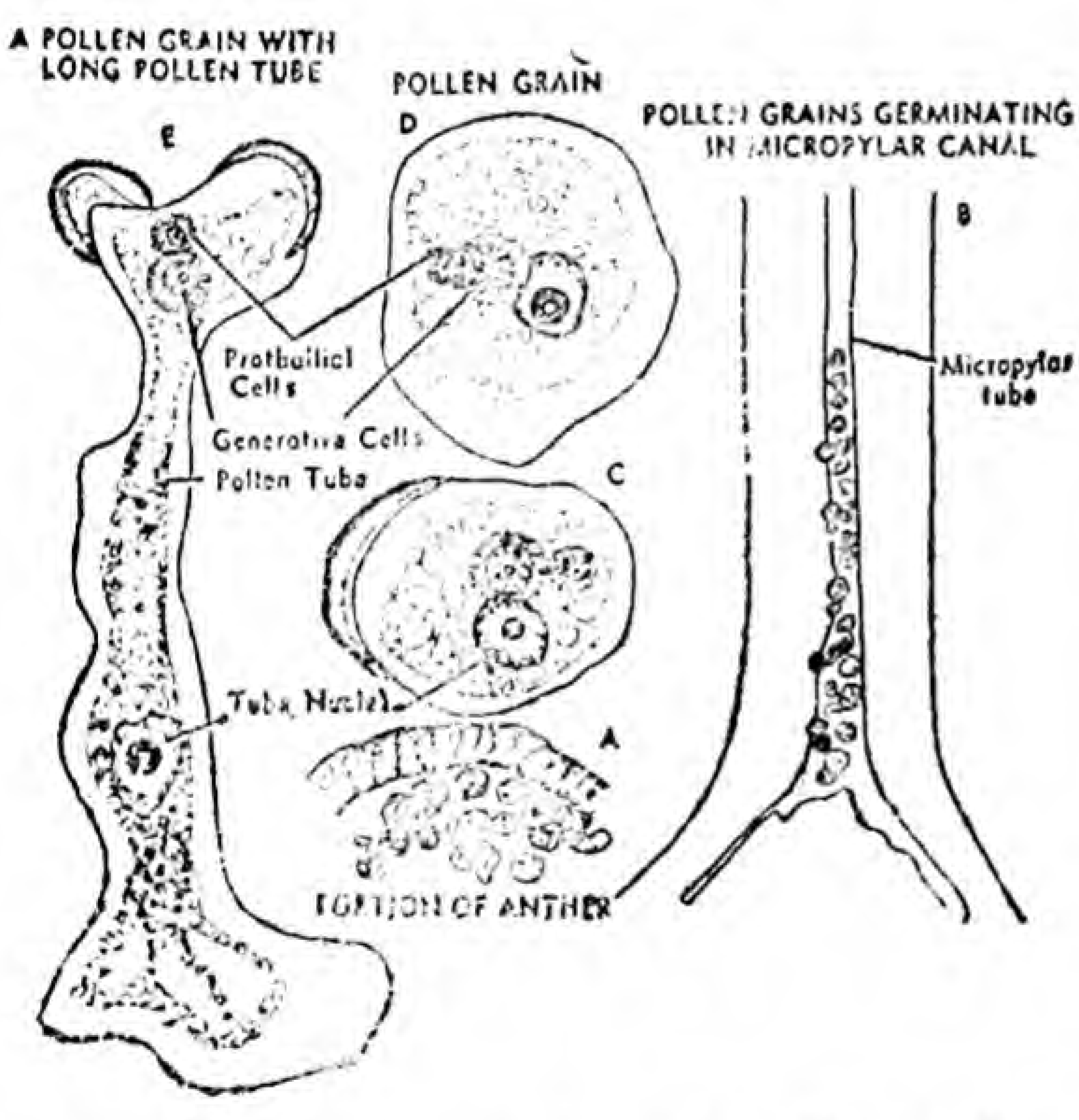



Fig. 9—27 Germination of pollen grains and the elongation of pollen tube inside the micropylar canal in *Gnetum gnemon* (After Madhulata). A–Portion of anther with pollen grains; B–Pollen grains inside the micropylar canal; C–Ruptured exine; D–A male gametophyte with prothallial, generative cells and a tube nucleus; D–An enlarged pollen tube.

Soon after the pollen grains reach the pollen chamber, the exine ruptures and intine protrudes in the form of a pollen tube (fig. 9-27 D&E) which may sometimes be branched. The generative nucleus later divides into two male cells or gametes (fig. 9-29 B), the latter are non-flagellate.

Thompson's view[2] (fig. 9-26) that there is no prothallial cell in the pollen of *Gnetum* has found no support in recent studies. It

1. Pijl, Van Der L. 1953.
2. Thompson, W. P. 1916

has been shown that there is a distinct cell wall which cuts off a cell and that this cell is a prothallial[1&2] cell (fig. 9-26).

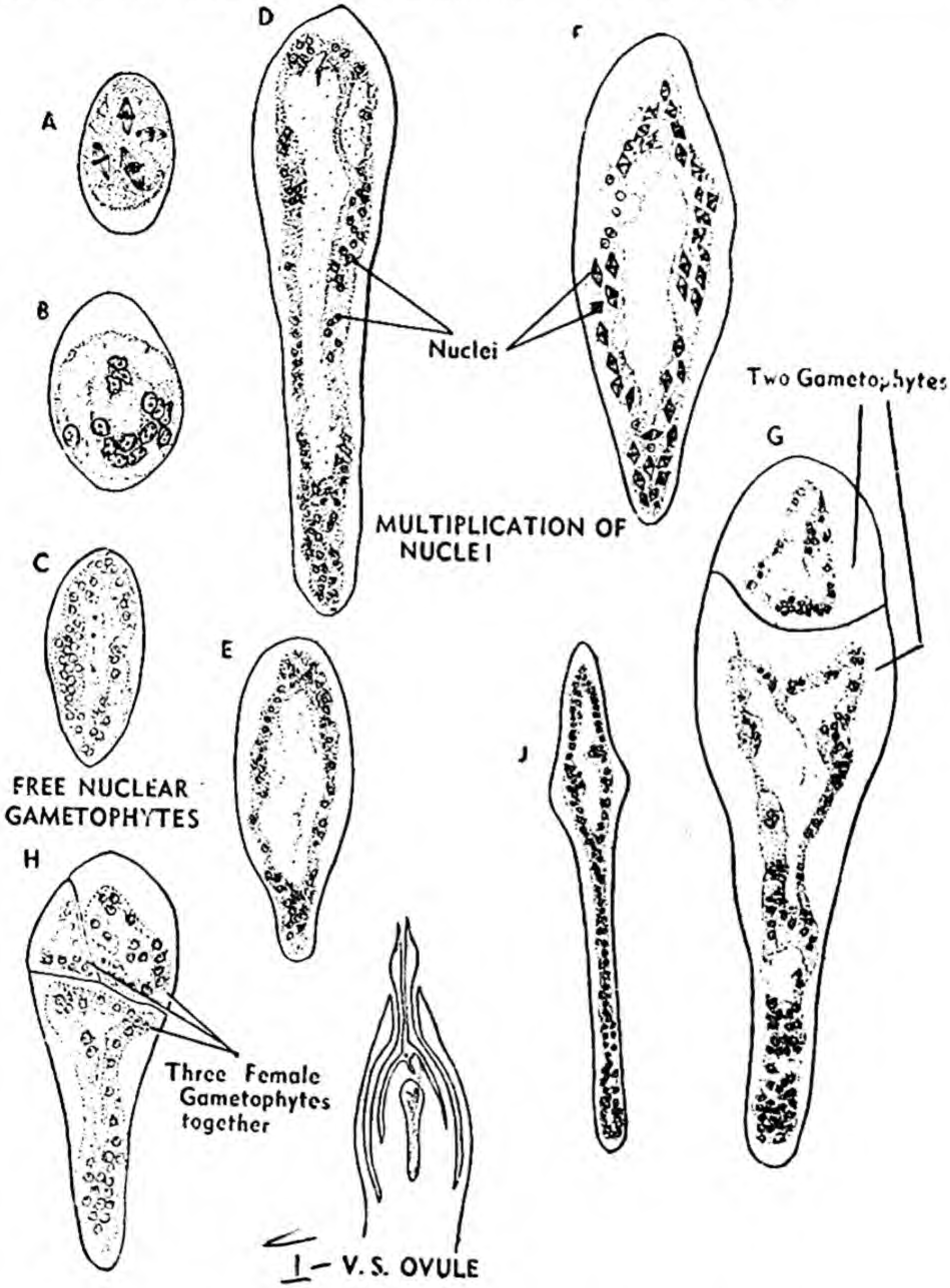



Fig. 9—28 Development of female gametophyte in *Gnetum ula* (After Vasil). A to F—Free nuclear stages [D—F show anenlarging central vacuole]; G and H—Shows the development of 2and 3 gametophytes respectively; I—V. S. of ovule with developing embryo; J—an abnormal female gametophyte.

1. Pearson, H. H. W. 1929.
2. Negi, V. & Madhulata 1957.

**Female gametophyte**—A large number of megaspore mother cells develop, though only a few, not more than two or three reach the sixteen-nucleate stage (fig. 9-28A&B); the others may degenerate or may persist till the differentiation of the egg. Now, the female gametophyte divides into a large number of nuclei by free nuclear divisions without walls making their appearance. A vacuole develops in the centre and the gametophyte elongates (fig. 9-28C-E). It now looks like an inverted flask (fig. 9-28 E&F), the lower part having most of the cytoplasm while the upper part has the vacuole. In *G. ula* it may become spindle-shaped. In *G. gnemon* up to 256, and in *G. ula* more than 1,500 nuclei have been counted. These are formed by free nuclear divisions. Many gametophytes at different stages of development may be present inside an ovule (fig. 9-28 G&H). They are usually present above the principal one and may soon degenerate (fig. 9-28 H). Sometimes an elongated spindle-shaped female gametophyte, tapering at both the ends, (fig. 9-28J) develops. This is an abnormality as the normal female gametophyte elongates towards the chalazal end only (fig. 9-28I).

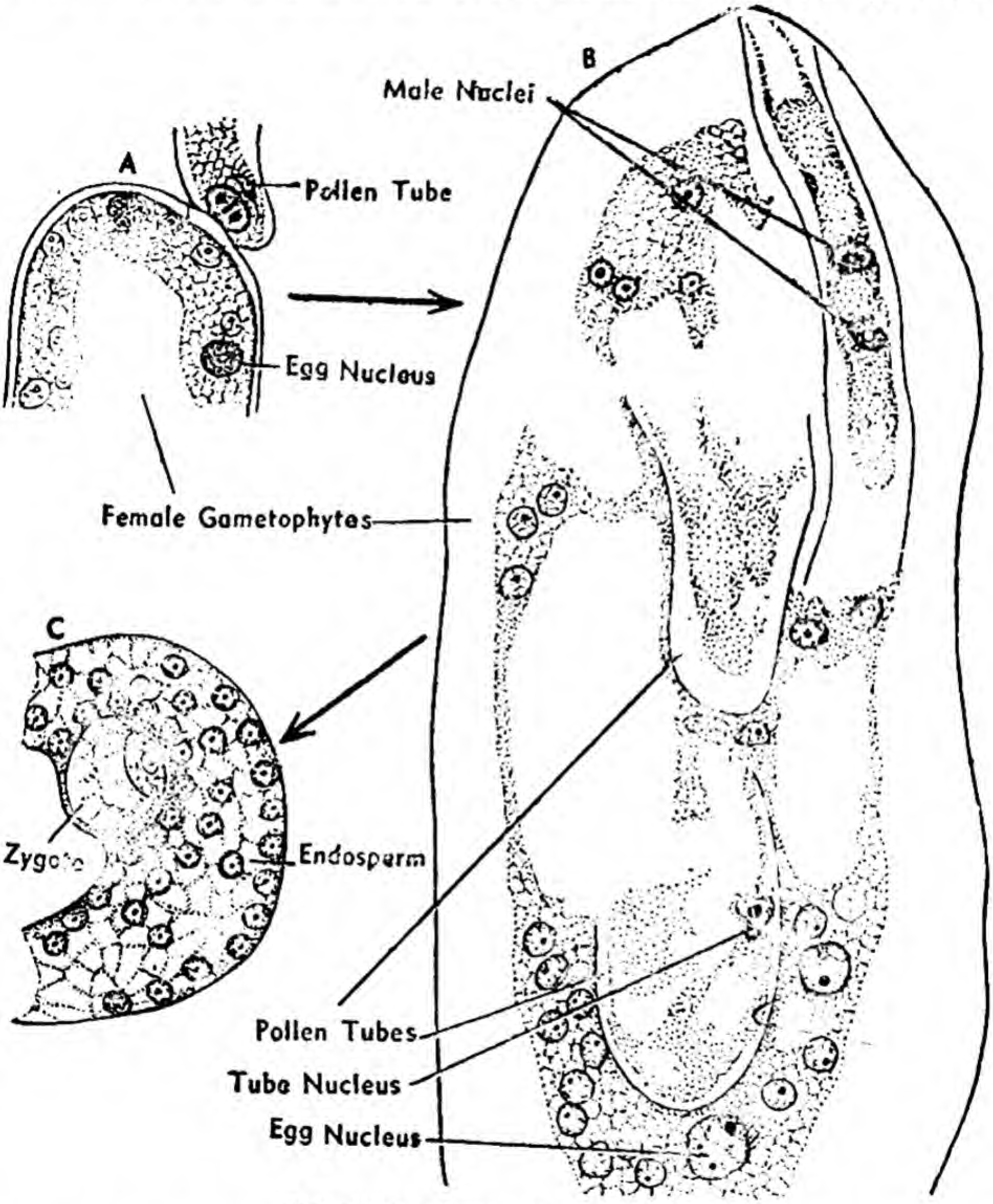
The nucellus, at the four nucleate stage of the female gametophyte, is massive and the gametophyte thus gets deeply buried in the nucellus. At the primary stage of meiosis a few nucellar cells situated below the gametophyte divide to form the radiating rows of cells called "the pavement tissue". It is usually consumed during the development of the gametophyte and is primarily meant for its nourishment.

Fagerlind[2] and Waterkeyn[3] reported 20 to 25 haploid chromosomes in *G. gaemon* and *G. africanum* respectively.

**Fertilization**—Several pollen grains germinate in the pollen chamber. In the pollen tube, the tube nucleus descends first. Later on the generative cell is organised (fig. 9-27E) which then divides to form two male cells. The pollen tubes pierce the nucellar tissue and reach the embryo sac. Archegonia are totally absent (fig. 9-29B). In *G. gnemon* the pollen tubes come in contact with the embryo sac after piercing the female gametophyte, not apically but laterally (fig. 9-29A). Usually two, rarely one or three

1. Coulter, J. M. 1908.
2. Fagerlind, F. 1941.
3. Waterkeyn, L. 1959.

nuclei of the female gametophyte enlarge. They have dense contents and have a tendency to absorb stains. These are egg nuclei which differentiate on being stimulated by the presence




FERTILIZATION IN GNETUM

Fig. 9—29 Stages of fertilization in *Gnetum*. A—Male and female gametes of *G. gnemon* are seen coming close together. The position of pollen tube is lateral (After Thompson); B—Elongation of several pollen tubes inside the female gametophyte in *G. gnemon* (After Thompson), C—Fusion of a male cell with an egg and the formation of a zygote in *G. africanum* (After Madhulata).

of the pollen tubes. The egg nucleus may attain a size 3 or 4 times larger than that of a normal vegetative nucleus. The male cells or gametes are released by the rupture of the pollen tube. Only one of them fuses with an egg and a zygote is formed(fig.9-29C).

Sometimes both the male cells which are non-flagellate may fuse with the two egg nuclei - if two eggs are present, thus more than one zygote may be formed. In *G. ula*, the method of egg maturation is slightly different. Here a few groups of cells, in the upper part of the gametophyte, each with 3 to 8 cells, differentiates. They have dense cytoplasm and occur near the pollen tubes. Only one or rarely two cells of each group function as egg, the rest degenerate and are used up in the nutrition of the developing egg. The development of more eggs continues even after an egg has been fertilized. The ovules on the male strobili are mostly abortive but may rarely produce normal ripe seeds.

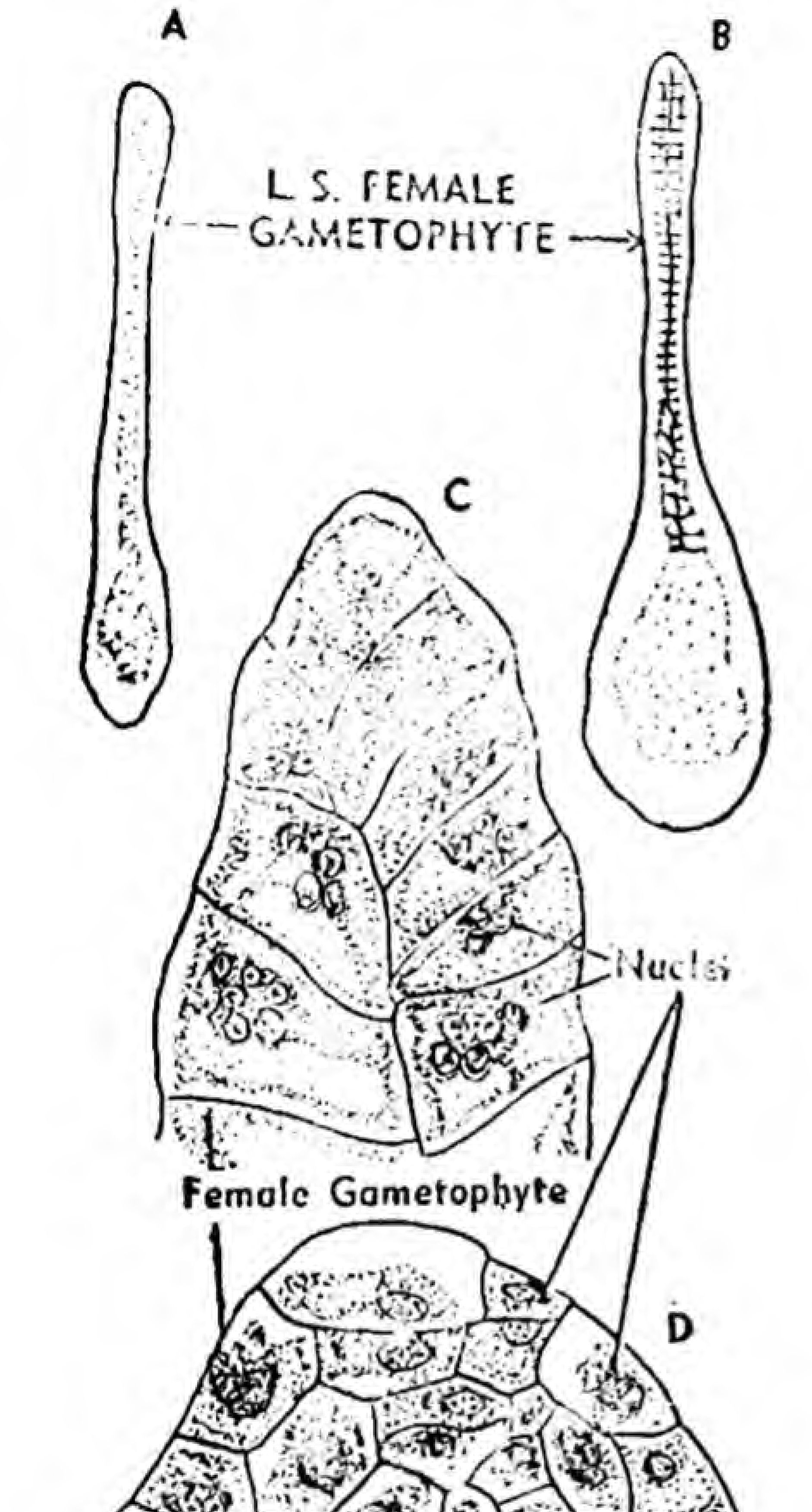



Fig. 9—30 Development of endosperm in *Gnetum ula* (After Vasil) A and B—L. S. of female gametophytes; C—Portions of endosperm showing multinucleate, and D—uninucleate as well as multinucleate chambers.

**Endosperm formation**—In *Gnetum* the gametophytic tissue starts developing before fertilization.The nuclei formed as a result of free nuclear divisions of the female gametophyte get enclosed by walls and form the so-called endosperm (fig. 9-30 A& C). This tissue, however, is cytologically quite different from the endosperm of the angiosperms. Some of the cells of the endosperm are uninucleate (fig. 9-30D) while others are multinucleate (fig. 9-30C& D). According to Madhulata[1] the wall formation is initiated either by fertilization or by the entry of pollen tube. She also

1. Madhulata, 1960.

observed that walls are first laid down at the chalazal end and then towards the micropylar end. Endosperm in *Gnetum* differs from similar tissue of other gymnosperms in the following respects :

(a) Cell wall formation is delayed till the pollen tubes enter the gametophyte ; (b) Presence of uni- and multinucleate i.e., polyploid cells; (c) Endosperm is formed by a few nuclei only.

DEVELOPMENT OF THE EMBRYO—Coulter[1] thought that the zygote undergoes free nuclear divisions. On the other hand, Thompson[2] stated that the first division of the zygote results in the formation of two cells which later form the embryo and the suspensor. Recent studies by Madhulata[3] reveal that the zygote in *G. gnemon* produces a protuberance on one end which grows down towards the endosperm tissue. Sometimes more than one protuberance may develop. The protuberances grows further to form a tube-like structure which undergoes septation to form several uninucleate cells. This tube later branches and forms the primary suspensor or the proembryonal tubes (fig. 9-31C&D) which grow towards the endosperm. In *G. ula* Apte and Kulkarni[4] and Vasil[5] observed that the primary suspensor tube cuts off a 'peculiar cell' (fig. 9-32) at its apex. The nucleus of the suspensor tube divides into two unequal daughter nuclei, the smaller of the two gets a wall round it and a lenticular 'peculiar cell' is thus formed

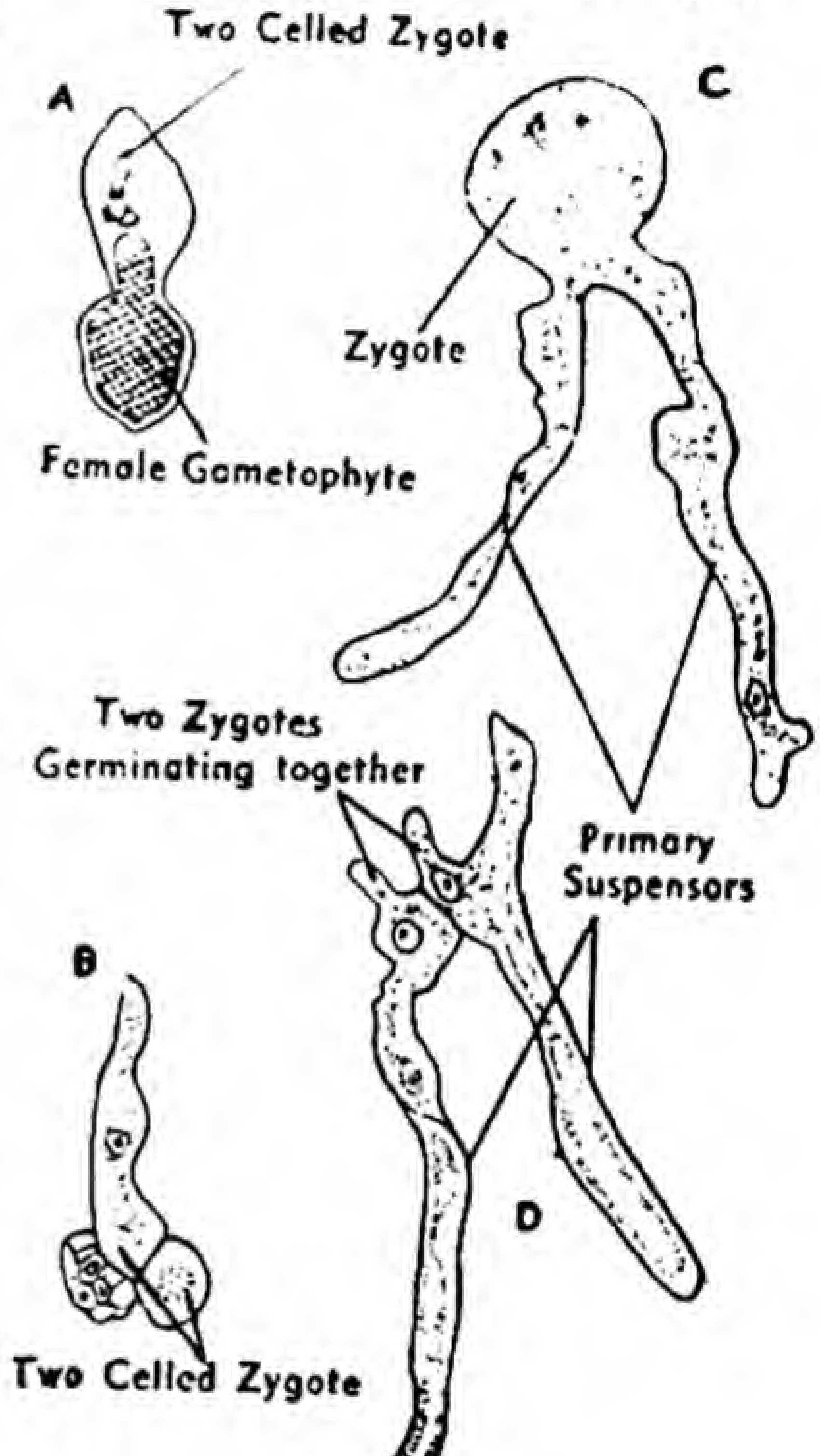



Fig. 9—31 Early stages of embryogeny in *Gnetum gnemon* (After Madhulata). A—V.S of female gametophyte; B—a two-celled zygote; C—a zygote with 2 primary suspensors; D—Two zygotes developing together.

1. Coulter, J. M. 1908.
2. Thompson, W. P. 1916.
3. Madhulata, 1960.
4. Apte, V. V. and L. H. Kulkarni 1953.
5. Vasil, V. 1959

(fig. 9-32). The larger nucleus of the suspensor tube degenerates. The seeds are usually shed at this stage. Further development of the embryo takes place on soil. The "peculiar cell" which is responsible for the formation of the embryo divides to form 2 cells both of which divide again to form a four-celled embryonal mass. The third division is transverse and thus an eight-celled embryo is formed. Further divisions are irregular. As the embryonal mass increases in size a few cells lying towards the primary suspensor tubes elongate to form the secondary suspensors. The cells lying at the lower end of the secondary suspensors later form the embryo proper.

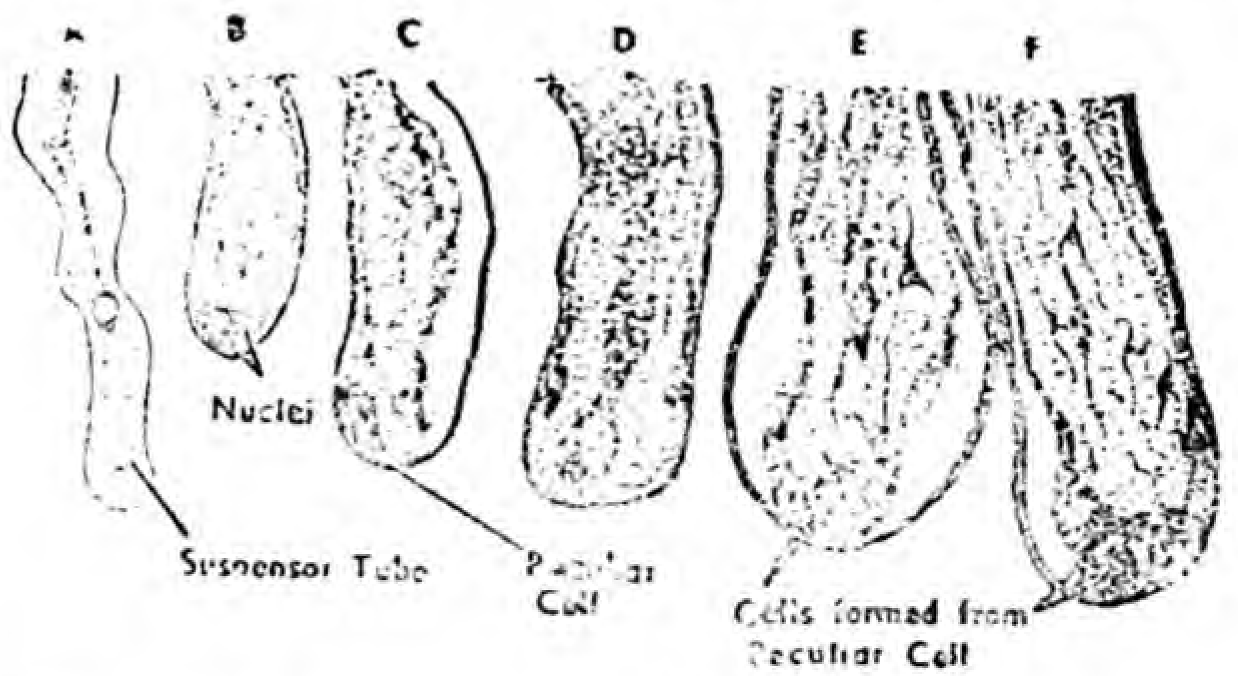



Fig. 9—32 Formation of peculiar cell and its further divisions in *Gnetum ula* (After Vasil).

The embryonal tip assumes conical form. The axis (future stem) is centrally situated at the apex of the embryonal mass. It is surrounded by two lateral cotyledons. Root-tip is formed at the opposite end of the axis. Simultaneously, a lateral hump, the so-called 'feeder' (fig. 9-36A), becomes prominent. Like the hypocotyl it develops an epidermis, cortex, vascular bundles and pith. The hypocotyl, when young, is longer than the feeder but soon the feeder outgrows the hypocotyl. The primary and the secondary suspensors degenerate and appear like fine threads. The "feeder" (fig. 9-36 A) remains inside the seed and is thought to pass on food to the developing embryo. Root is protected by a root cap. Cotyledons on maturity turn orange-pink in colour. Laticiferous ducts and stomata also develop afterwards.

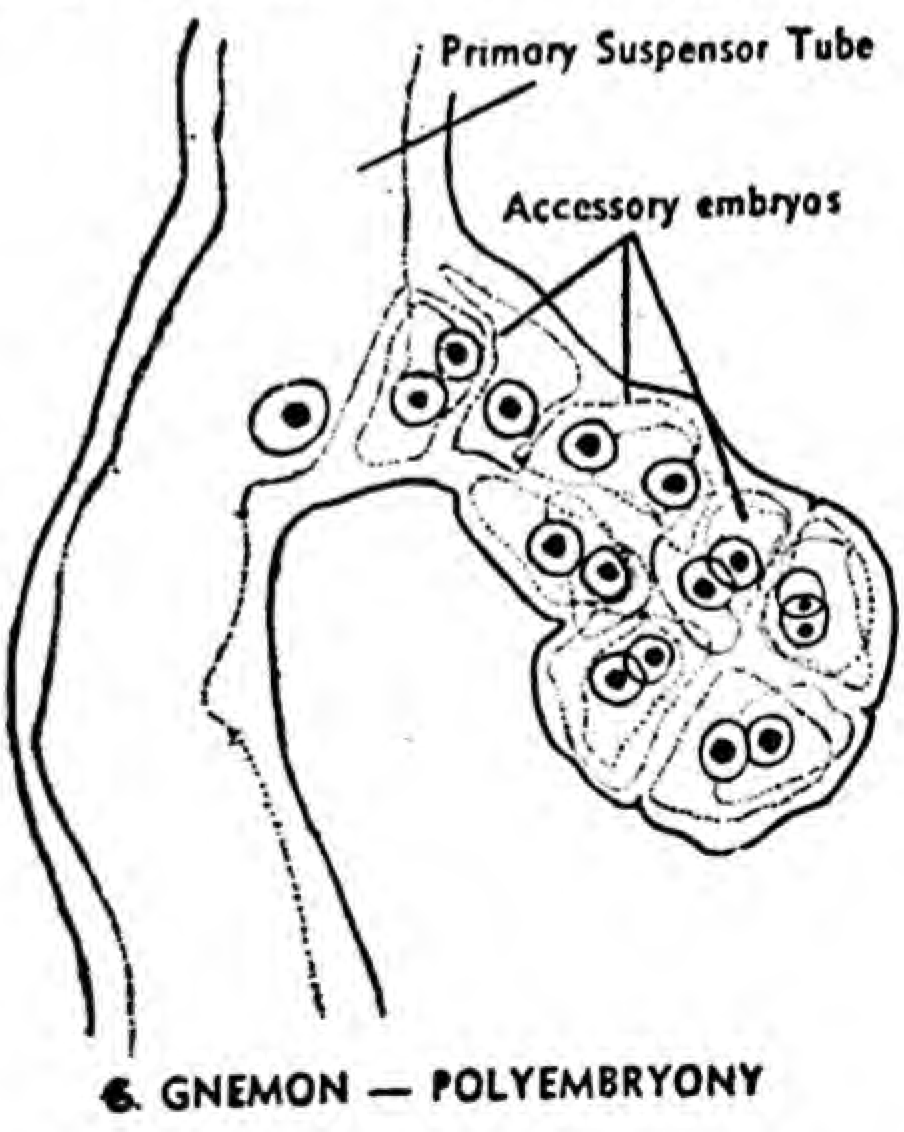



Fig. 9—33 A stage of polyembryony in *Gnetum gnemon* with accessory embryos (After Madhulata).

**Polyembryony**—Bower[1], Haining[2], Vasil[3] and Madhulata[4] have reported a few instances of polyembryony in *G. ula* and *G. gnemon* but usually only one embryo attains maturity, the rest perish. Polyembryony occurs either due to proliferation of the secondary suspensors or as a result of their budding (fig. 9-33).

**Structure of the seed**—In *G. gnemon* the seed is oval or elongate and green to red in colour (fig. 9-34). Nucellus of the female gametophyte, once massive, now becomes a thin strip at the apex. The seed is surrounded by three distinct layers of envelope (fig-9-35). Studies made by Thoday[5] reveal that the outermost layer of the envelope is free from base to apex; it is green and fleshy and is made up of parenchymatous cells. It possesses irregularly distributed sclereids and stomata (fig. 9-35). The middle layer of envelope (=outer integument) is hard and it forms the protective layer of the seed. It grows above the outer one and surrounds the micropylar tube. It is traversed by numerous vascular bundles which branch at intervals. It possesses distinct palisade and also the lignified and parenchymatous cells. The innermost layer of the envelope (= inner integument) is coalescent with the nucellus up to 2/3rds of its length. Its free part encircles the nucellar cap and projects beyond the nucellus. It is composed of thin-walled parenchymatous and lignified cells and numerous vascular bundles traverse it. Within the innermost layer of the envelope in *G. africanum* lies the massive endosperm which projects upwards

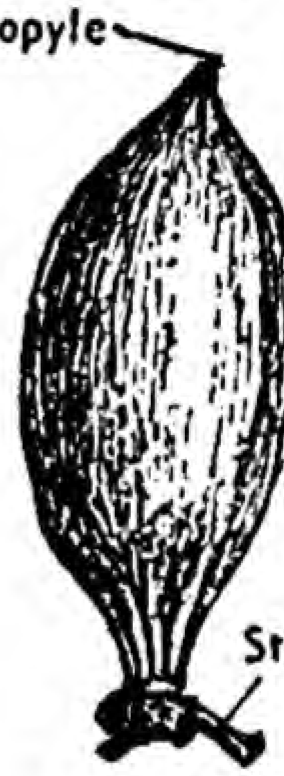



Fig. 9-34 A seed of *Gnetum gnemon* from Malaya.

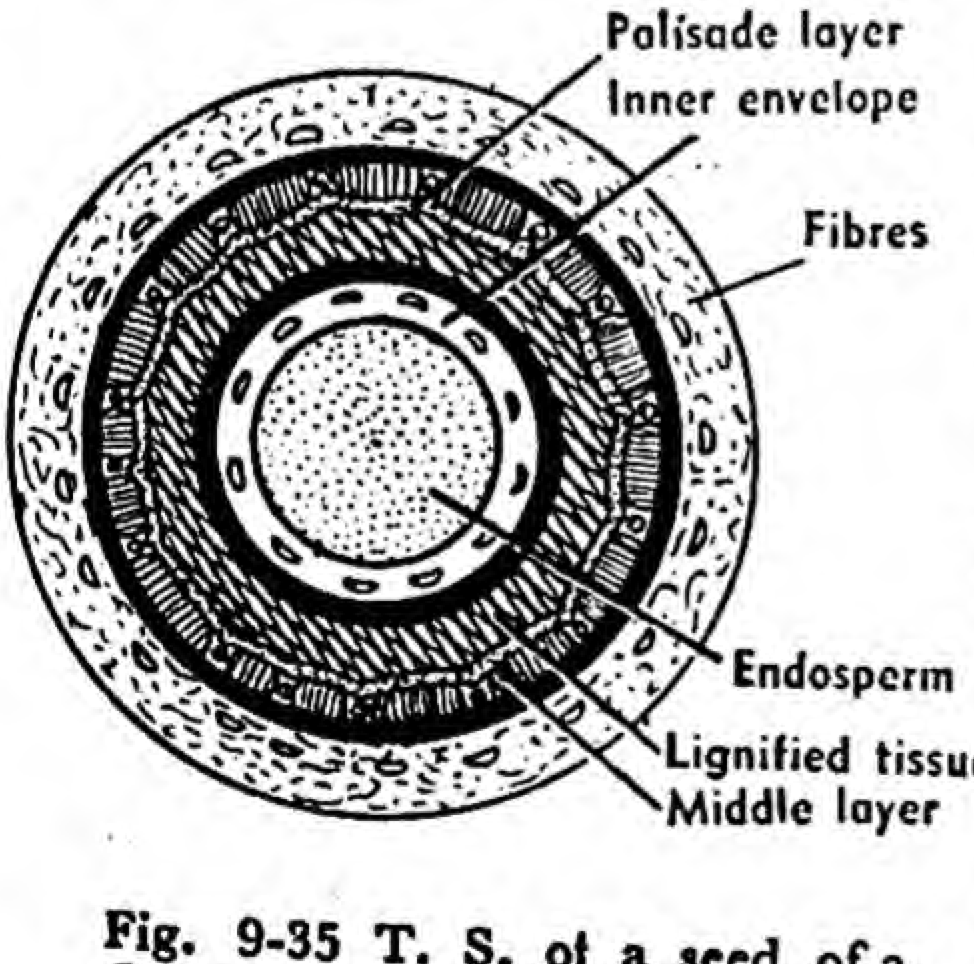



Fig. 9-35 T. S. of a seed of a *Gnetum africanum* (After Thoday).

1. Bower, F. O. 1882.
2. Haining, H. I. 1920.
~~3. Vasil, V. 1959.~~
4. Madhulata 1960.
5. Thoday, M. G. Sykes 1911.

in the form of a 'tent pole'. It has thick and lignified walls and it supports the nucellar cap. The structure is not known to occur in the Indian species.

**Germination of the seed**—The seed is shed at a stage when the secondary suspensors are differentiating. The maturation of the seed takes place when it has fallen to the ground. Negi[1] reported that the seeds in *G. ula* germinate about 11-12 months after being shed from the mother plant. During germination, the root along with its cap emerges first, it then bends down, enters into the soil and develops the tap root system (fig. 9·36 B,D&E). Soon the hypocotyl elongates and pushes the two cotyledons out of the seed (fig. 9-36E,F&G). Germination is epigeal. Cotyledonary leaves turn green and resemble ordinary foliage leaves. Next, the stem tip expands and forms the first pair of plumular leaves (fig. 9-36G). "Feeder" still remains inside the seed.

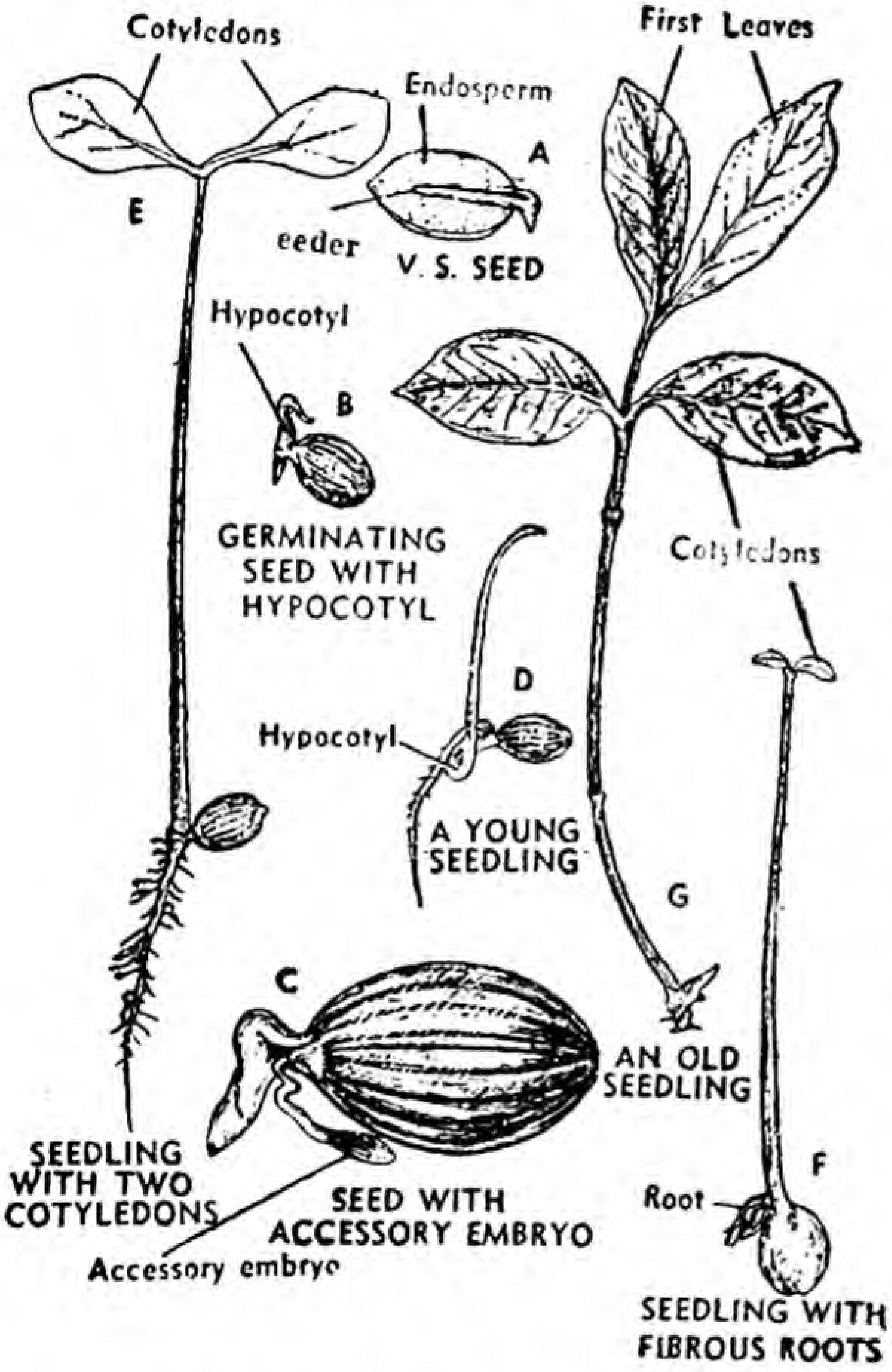



Fig. 9-36 Stages of seed germination in *Gnetum gnemon* (After Madhulata).

ECONOMIC IMPORTANCE—The seed kernels of *G. gnemon* are moulded into cakes and biscuits. Young leaves and strobili are used as vegetables. *G. ula* is also a source of edible oil. The oil is said to possess antirheumatic properties and is used for massage. Bark of *G. latifolium* yields strong fibres which are used

1. Negi, V. 1958.

for making nets and ropes. Fibre pulp is used in manufacturing paper. *G. montanum* is reported to possess piscidal properties.

## AFFINITIES OF THE GNETALES

Different genera of the order possess resemblances with the true gymnosperms on the one hand and the angiosperms on the other. These resemblances may be summarized as below :

RESEMBLANCES WITH THE GYMNOSPERMS—Ovary being absent, the ovules remain naked. Style and stigma are absent but in *Welwitschia* there occurs a tube-like extension resembling a style. Pollen grains enter through the micropyle and get directly lodged on the surface of the nucellus, not on the stigma, a typical gymnospermous character. The pollen grain consists of a prothallial cell and two male cells; there is no stalk cell and body cell in *Gnetum*; tube nucleus is reduced and is without a wall. In all the three genera of the Gnetales, tracheids with bordered pits in the xylem, and sieve cells in the phloem are present. The mode of pollination is anemophilous. The endosperm is a haploid or polyploid tissue and starts developing before fertilization. Simple or cleavage types of polyembryony may occur. Fruit formation is absent.

RESEMBLANCES WITH THE ANGIOSPERMS—The leaves are broad and green possessing reticulate venation. They are arranged in an opposite-decussate manner. The climbing or tree-like habit of *Gnetum* occurs in the angiosperms. Vessels similar to those of the angiosperms occur together with the tracheids in the secondary xylem of all the three genera of the Gnetales. Archegonia are totally absent from the female gametophyte of *Gnetum*. The development of the female gemetophyte in *Gnetum* is tetrasporic. Free nuclear divisions occur in the embryosac. In *Gnetum* the endosperm completes its development after fertilization.

# BIBLIOGRAPHY


**Andrews, H. N. Jr. 1955.** Index of Generic Names of Fossil Plants, 1820-1950. *Geol. Surv. Bull.* 1013.

**———1961.** *Studies in Palaeobotany.* John Wiley & Sons Inc. New York, London.

**Apte, V. V. & L. H. Kulkarni 1953.** Some observations on *Gnetum ula* Brongn. found in Western Ghats. *Curr. Sci.* **22** : 261-262.

**Arber, E. A. N. 1919.** Remarks on the organization of the cones of *Williamsonia gigas* (L & H). *Ann. Bot.* **33**: 173-179.

**Arnold, C. A. 1947.** *An Introduction to Palaeobotany.* McGraw Hill Co. Inc. New York, London.

**———1948.** Classification of Gymnosperms from the point of view of Palaeobotany. *Bot. Gaz.* **110**: 2-12.

**———1953.** Origin and relationships of cycads. *Phytomorphology* **3**: 51-65.

**Atwood, S. 1936.** The anomalous root structure of *Cycas revoluta. Amer. J. bot.* **23**: 336-340.

**Bailey, L. W. 1953.** Evolution of tracheary tissue of land plants. *Amer. J. bot.* **40**: 4-8.

**Bannan, M. W. 1965.** Ray contacts and rate of anticlinal division in fusiform cambial cells of some Pinaceae. *Canad. J. bot.* **43** (5) : 503-504.

**Battaglia, E. 1953.** The male and female gametophytes of angiosperms—an interpretation. *Phytomorphology* **1**: 87-116.

**Beccari, O. 1877.** Della organogenia dei fiori feminei del *Gnetum gnemon Nuovo G. bot. Ital.* **9**: 91-99.

**Benson, M. 1908.** On the contents of the pollen chamber of a specimen of *Lagenostoma ovoides. Bot. Gaz.* **45**: 409-412.

**Bharadwaja, R. C. 1957.** Genus *Gnetum* Linn. in India, Pakistan and Burma. *J. Indian bot. Soc.* **36**: 408-420.

**Beck, Charles, B. 1966.** On the origin of Gymnosperms. *Taxon.* **15** (9): 337-339.

**Bessey, C. E. 1902.** The morphology of pine cone. *Bot. Gaz.* **33**: 157-159.

**Bierhorst, D. W. 1960.** Observations on tracheary elements. *Phytomorphology* **10**: 249-305.

**Bor, N. L. 1953.** *Manual of Indian Forest Botany.* Oxford Univ. Press, London.

Bower, F. O. 1882. The germination and embryogeny of *Gnetum gnemon*. *Quart. J. micr. Sci.* 22: 278-298.

Boyle, P. & J. Doyle 1954. Development of *Podocarpus nivalis* in relation to other Podocarps II Embryogeny in *Eupodocarpus*. *Sci. Proc. Roy. Dubl. Soc.*, 26: 289-312.

Brown, W. H. 1935. *The Plant Kingdom*. Ginn & Co. New York, U.S.A.

Buchholz, J. T. 1931. The pine embryo and embryos of related genera. *Trans. Illinois Acad. Sci.* 23: 117-125.

Burns, M. A. 1964. *Plant Anatomy*. Bk. 1. London.

Calvin, M. 1964. Chemical evolution. *Proc. Tenth intern. Bot. Cong.*: 41-56

Carter, M. Geraldine 1911. A reconsideration of the origin of transfusion tissue. *Ann. bot.* 25: 975.

Chamberlain, C. J. 1935. *Gymnosperms, Structure and Evolution*. Chicago.

Chaudhuri, H. & A. R. Akhtar 1931. The coral roots of *Cycas revoluta*, *Cycas circinalis* and *Zamia floridana* and the algae inhabiting them. *J. Indian bot. Soc.* 10: 43-59.

Coulter, J. M. 1908. The embryo sac and embryo of *Gnetum gnemon*. *Bot. Gaz.* 46: 43-49.

———& C.J. Chamberlain 1910. *Morphology of Gymnosperms*. Chicago.

Coulter, M. C. & H. J. Dittmer 1964. *The Story of Plant Kingdom*. 3rd Ed. Chicago, Illinois.

Cronquist, A., A. Takhtajan, W. Zimmermann 1966. On the higher taxa of Embryobionta. *Taxon* 15 (4): 129-134.

Dallimore, W. & A. B. Jackson 1948. *Hand Book of Coniferae*. 3rd Ed. London.

De Bary. A. 1884. *Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns*. Oxford. Eng. trans.

Delevoryas, T. 1953. A new male Cordaitean fructification from the Kansas, Carboniferous. *Amer. J. bot.* 40: 144-150.

———1963. Investigations of North American Cycadeoids. Cones of *Cycadeoidea*. *Amer. J. bot.* 50 (1): 45-52.

———1965. Investigations of North American Cycadeoids : Microsporangiate structures and phylogenetic implications *Palaeobotanist* 14: 89-93.

———1968. Investigations of North American Cycadeoids: Structure, ontogeny and phylogenetic considerations of cones of *Cycadeoidea*. *Palaentographica* 121 (4-6) Abt. B: 122-133.

De Silva, B. L. T. & M. S. Tambiah 1952. A contribution to the life-history of *Cycas rumphii Mic*. *Ceylon J. Sci. A* 12: 1-22.

**Dogra, P. D. 1964.** Pollination mechanisms in Gymnosperms *Advan. Palynology. Nat. Bot. Gdn.* Lucknow:142-175.

———**1964.** Gymnosperms of India II. Chilgoza pine (*Pinus gerardiana* Wall.) **109,** *Nat. Bot. Gdn.* Lucknow.

———**1966.** Observations on *Abies pindrow* with a discussion on the question of the occurrence of apomixis in Gymnosperms. *Silvae Genetica* **15** (1): 11-20.

———**1967.** Seed Sterility and Disturbances in Embryogeny in Conifers with particular reference to Seed Testing and Tree Breeding in Pinaceae. *Studia Forestalia Suecica* Nr. **45.**

**Doyle, J. 1957.** Aspects and Problems of conifer embryology *Advan. Sci.* **14** (54): 120-130.

———**1963.** Polyembryogeny in *Pinus* in relation to that in other conifers—A survey-*Proc. Roy. Irish Acad.* **62** (B) : 181-216.

**Dupler, A. W. 1917.** The gametophytes of *Taxus canadensis* Marsh. *Bot. Gaz.* **64** (2): 115-136.

———**1919.** Staminate strobilus of *Taxus canadensis* Marsh. *Bot. Gaz.* **68** (5): 345-366.

———**1920.** Ovuliferous structures of *Taxus canadensis Bot. Gaz* **69** (6): 492-520.

**Duthie, A. V. 1912.** Anatomy of *Gnetum africanum. Ann. Bot.* London **26:** 593-603.

**Dutt, B. S. M. 1952.** On the abnormal cones of *Gnetum Linn. Sci. Cult.* **18:**199.

**Eames, A. J. 1936** *Morphology of Vascular Plants* (lower group). McGraw Hill Co. New York.

———**1952.** Relationships of Ephedrales. *Phytomorphology* **2:** 79-100.

———**& L. H. McDaniels 1947.** *An introduction to Plant anatomy.* 2nd. Ed. McGraw Hill Co., New York.

**Eichler, A.W 1889.** Coniferae in Engler und Prantl's Die natürlichen Pflanzenfamilien II Tiel.

**Engler, A. und K. Prantl 1889.** *Die Natürlichen Pflanzenfamilien* II Tiel.

**Esau, K. 1953.** *Plant Anatomy.* II Print. New York, London.

**Fagerlind, F. 1941.** Bau und Entwicklung der *Gnetum*—Gametophyten. *K. Svenska Vetensk. Akad. Handl.* **19** (8): 1-55.

**Favre-Duchartre, M. 1958.** *Ginkgo.* An oviparous plant. *Phytomorphology* **8** (3 & 4):377–390.

**Ferguson, M. C. 1904.** Contributions to the knowledge of the life-history of *Pinus* with special reference to sporogenesis, the development of gametophytes and fertilization. *Proc. Wash, Acad. Sci.* **6**: 1-202.

**Florin, R. 1931.** Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. I. Morphologie und Epidermisstruktur der Assimilationorgane bei den rezenten Koniferen. *K. Svenska. Vetensk. Akad. Handl.* **10** (1): 1-588.

**——1948.** On morphology and relationships of Taxaceae. *Bot. Gaz.* **110**: 31-39.

**——1951.** Evolution in Cordaites and Conifers. *Acta. Horti. Bergiana.* **15**: 285-388

**Foster, A. S. & E. M. Gifford 1959.** *Comparative Morphology of Vascular Plants.* San Francisco.

**Gifford, E. M. 1943.** The structure and development of shoot apex of *Ephedra ultissima* Desf. *Bull. Torr. bot. Club.* **70**: 15-25.

**Greguss, P. 1955.** *Identification of living Gymnosperms on the Basis of Xylotomy.* Budapest.

**——1958.** Some recent data on the xylotomy of *Cycas, Zamia* and *Ginkgo. Acta. Biol.* N. S. **4** (3, 4): 143-147.

**Haining, H. I. 1920.** Development of embryo of *Gnetum. Bot. Gaz.* **70**: 436-445.

**Harris, T. M. 1932.** The fossil flora of Scoresby Sound East, Greenland Pt. 3. Caytoniales and Bennettitales. *Med. om Grönland.* **85** (5): **1-30.**

**——1944.** A revision of *Williamsoniella. Phil. Trans. Roy. Soc.* London. **231-B**: 313-328.

**Hill, A. F. 1951.** *Economic Botany.* McGraw Hill & Co., New York.

**Hooker, J. D. & B. D. Jackson 1895-1950.** *Index Kewensis.*

**Hui Lin Li 1952.** Present distribution and habitats of the Conifers and Taxads. *Evolution.* VII (3): 245-261.

**Jeffery E. C. 1917.** *The Anatomy of Woody Plants.* Chicago.

**Johnson, L. A. S. 1959.** The families of Cycads and the Zamiaceae of Australia. *Proc. Linn. Soc. N. S. W.* **84**: 64–117.

**Johnson, M. A. 1951.** The shoot apex in Gymnosperms. *Phytomorphology* **1**: 188-203.

**Kanis, A. & W. K. H. Karstens 1963.** Amphistomatic leaves in *Ginkgo. Acta. Bot. Neerl.* **12**: 281-286.

**Khan, R. 1940.** A note on double fertilization in *Ephedra foliata. Curr. Sci.* **9**: 323-324.

Khan, R. 1943. Contributions to the morphology of *Ephedra foliata* Boiss II. Fertilization and embryogeny. *Proc. nat. Acad. Sci. India* 13: 357-375.

Khoshoo, T. N. 1961. Chromosome numbers in Gymnosperms. *Silvae. Genetica.* 10: 1-32.

Konar, R. N. 1960. Morphology and embryology of *Pinus roxburghii* Sar. *Phytomorphology* 10: 305-319.

———& S. Ramchandani 1958. Morphology and embryology of *Pinus wallichiana* Jack. *Phytomorphology* 3: 328-346.

Kubart, B. 1905. Die wiebliche Bliithe von *Juniperus communis* Linn. *Sitzungsber. Kais. Acad. Wiss. Wien.* 114: 29.

Land, W. J. G. 1904. Spermatogenesis and Oögenesis in *Ephedra trifurca. Bot. Gaz.* 38: 1-18.

———1907. Fertilization and embryogeny in *Ephedra trifurca. Bot. Gaz.* 44: 273-292.

La Rue, C. D. 1948. Regeneration in megagametophyte of *Zamia floridana. Bull. Torr. Bot. Club.* 75: 597- 603.

————1950. Regeneration in megagametophyte of *Cycas. Amer. J. bot.* 37: 664.

Lignier, O. 1892. La nervation taenlopteridee des folioles de *Cycas* et le tissue de transfusion, *Bull. Soc. Linn. Normandie.* 4e ser., 6: 65-71.

Long. A. G. 1944. On the prothallus of *Lagenostoma ovoides Will. Ann. Bot.* 8: 105-117.

———1960. *Stamnostoma huttonense* gen. et. sp. nov, "A Pteridosperm seed & cupule from the calciferous sandstone series of Berwickshire *Trans. Roy. Soc. Edin.*, 64: (9): 201-215.

———1960. "On the structure of *Samaropsis scotica* Calder (emended) and *Eurystoma angulare* "gen. et. sp. nov., petrified seeds from the calciferous sandstone series of Berwickshire. *Trans. Roy. Soc. Edin.*, 64 (13): 261-280.

———1961. *Tristichia ovensi* gen. et, sp. nov., A protostelic Lower Carboniferous Pteridosperm from Berwickshire & East Lothian, with an account of some associated seeds and cupules. *Trans. Roy. Soc Edin.* 44 (18): 477-489,

Lubbock, Sir John Bart 1892. *A Contribution to Our Knowledge of Seedlings.* London,

Madhulata 1960. Morphology and embryology of *Gnetum gnemon L.* (In Maheshwari's *Gnetum. Botanical monograph* No. 1. C. S. I. R. New Delhi)

Maheshwari, P. 1935, Contributions to the morphology of *Ephedra foliata* Boiss. I. The development of the male and female gametophytes. *Proc. Indian Acad. Sci.*, 1: 586-606.

**Maheshwari, P. 1950.** *An Introduction to the Embryology of Angiosperms* New York.

———**1953.** Abnormal cones of *Gnetum. Sci. & Cult.* **18**: 390.

———**& V. Vasil 1961 a.** The stomata of *Gnetum. Ann. Bot.* London **25** (99): 313-319.

———**1961b**. *Gnetum*. Botanical monograph No, I. C. S. I. R. New Delhi.

**Marsden, M. P. F. & T. A. Steeves 1955.** On the primary vascular and nodal anatomy of *Ephedra*. *J. Arnold Arbor.* **36**: 241-258.

**McLean, R. C. & W. R. Ivimey Cook 1951.** *Text-book of Theoretical Botany*. I: London.

**Mc William, J. R. 1958.** The role of micropyle in the pollination of *Pinus. Bot. Gaz.* **120** (2): 109-117.

**Miller, W. L. 1919.** Polyxylic stem of *Cycas media. Bot. Gaz.* **68**: 208-221.

**Mulay, B. N. 1941.** A study of the pistillate flowers of *Ephedra foliata* Boiss. found on Drigh Road near Karachi in Sind. *Proc. Indian Sc. Cong.* **28** (3): 158.

**Nathorst, A. G. 1911.** Palaeobotanische Mitteilungen. I. *Kungl. Svenska Veteskapsakad.* Handl., **46** (4): 1-33.

**Negi, V. 1958,** Morphology and embryology of *Gnetum ula* Brongn. (In Maheshwari's *Gnetum Botanical* monograph No. 1. C. S. I. R. New Delhi)

—**& Madhulata 1957.** Male gametophyte and megasporogenesis in *Gnetum. Phytomorphology.* **7**: 230-236.

**Nostog, K. & Rose Overstreet 1965.** Some observations on the gametophytes of *Zamia integrifolia. Phytomorphology.* **15**: 46 49

**Oliver, F. W. & D. H. Scott 1904.** *Lagenostoma. Phil. Trans. Roy. Soc. B.* **197**: 193-247.

**Pant, D. D. 1953.** Notes on *Cycas* plants growing at Allahabad. *J. Indian boc. Soc.* **32**: 145-156.

———**1957.** The classification of Gymnospermous plants, *Palaeobotanist.* **6** (1): 65-70.

———**& B. Mehra. 1962.** *Studies in Gymnospermous plants. Cycas.* Allahabad.

———**& D. D. Nautiyal 1953.** Cuticular and epidermal studies of some modern cycadean leaves. Sporangia and seeds (In Pant's *Studies in Gymnospermous plants, Cycas.* Allahabad)

**Pearson, H. H. W. 1912.** On the microsporangium and microspore of *Gnetum* with some notes on the structure of inflorescence, *Ann. Bot.* London **26**: 603-620.

**Pearson, H. H. W. 1929.** *Gnetales.* Cambridge.

**Pettit, J. M. 1966.** The megaspore membrane in some gymnospermous ovules. *J. Linn. Soc. Lond.* **59** (379): 253-263.

**Pilger, R. 1926.** Gymnospermae in Engler, A. und K. Prantl's *Die Natürlichen Pflanzenfamilien.* II. Tiel.

**Pijl, Van Der L. 1953.** On the flower biology of some plants from Java with general remarks on fly-traps (species of *Annona, Artocarpus, Typhonium, Gnetum, Arisaema,* and *Abroma Ann. Bogor.* **I**: 77-99.

**Potonié, H. 1902.** Cycadofilicales, in Engler und Prantl's *Die Natürlichen, Pflanzenfamilien.* **I**: 780-798.

**Raizada, M. B. & K. C. Sahni 1960.** Living Indian Gymnosperms, Part I. *Indian Forest Rec.* Botany, **5** (2). Delhi.

**Rao, L. N. 1961.** Life-history of *Cycas circinalis.* Pt. I *J. Indian bot. Soc.* **40** (4): 601-619.

———**1963.** Life-history of *Cycas circinalis,* Pt. II *J. Indian bot. Soc.* **42** (2): 319-332.

**Rodin, R. J. 1966.** Leaf structure and evolution in American species of *Gnetum. Phytomorphology.* **16**: 56-68.

**Sachs, J. 1882.** *Text-book of Botany.* Second Ed.

**Sahni, B. 1920.** On the structure and affinities of *Acmopyle pancheri* Pilger. *Phil. Trans. Roy. Soc.* London. **210 B**: 253-310.

———**1932.** A petrified *Williamsonia* (*W. sewardiana* sp. nov.) from the Rajmahal Hills, India. *Mem. geol. Surv. India, Palaeont. Indica* n. s., **20** (3): 1-19.

**Schuster, J. 1932.** Cycadaceae IV. *Das Pflanzenreich* I.

**Scott, D. H. 1962.** *Studies in Fossil Botany.* III Ed, New York.

**Seeliger, I. 1954.** Studien am Sprossvegetationskegel von *Ephedra fragilis* var. *campylopoda* (C. A. Mey) Stapf. *Flora,* **141**: 114-162.

**Sethi, M. L. 1928.** Contribution to our knowledge of the life-history of *Pinus longifolia. J. Indian bot. Soc.* **7** (1): 105-150.

**Shetty, B. V. & K. Subramanyam 1962.** Cytology of *Cycas. Proc. Indian Sci. Cong.* Pt. III (Abstract): 259.

**Sifton, H. B. 1915.** On the occurrence and significance of the 'bars or rims' of Sanio in the cycads. *Bot. Gaz.* **60**: 400-405.

**Sitholey, R. V. 1963.** Gymnosperms of India, I. Fossil forms. *Bull. Nat. Bot. Gdn.* **86** Lucknow.

———**& M. N. Bose 1953.** *Williamsonia santalensis,* sp. nov. A male fructification from the Rajmahal Series with remarks on the structure of *Ontheanthus polyandra* Gunju, *Palaeobotanist* **2**: 29-39.

**Smith, F. G. 1907.** Morphology of the trunk and development of the microsporangium of cycads. *Bot. Gaz.* **43**: 187-204.

**Sporne, K. R. 1965.** *The Morphology of Gymnosperms.* Hutchin. Univ. Lib. London.

**Sterling, C. 1948.** Gametophytic development in *Taxus cuspidata. Bull. Torr. Bot. Club,* **75** (2): 147-165.

———**1963.** Structure of male gametophyte in Gymnosperms *Biol. Rev.* **38**: 167-203.

**Strasburger, E. 1872.** Die Coniferen und die Gnetaceen.

**Swamy, B. G. L. 1948.** Contribution to the Life-history of a *Cycas* from Mysore (India). *Amer. J. bot.* **35**: 77-88.

**Takeda, H. 1913.** A theory of transfusion tissue. *Ann. Bot.* London **27**: 359-363.

———**1913.** Development of the stoma in *Gnetum gnemon. Ann. Bot.* London. **27**: 365-366.

**Thoday, M. G. (Sykes) 1911.** The female inflorescence and ovules of *Gnetum africanum,* with notes on *G. scandens. Ann. Bot.* London **25**: 1101-1135.

———**1921.** Anatomy of the ovule and seed in *Gnetum gnemon,* with notes on *G. funiculare. Ann. Bot* London. **35**: 37-53.

**Thomas, H. H. 1913.** The fossil flora of the Cleveland Dt. *Quart. J. geol. Soc.* London. **59**: 223-251.

———**1915.** On *Williamsoniella,* a new type of Bennettitalean flower. *Phil. Trans. Roy. Soc.* London **207-B**: 113-148.

———**& N. Bancroft 1913.** On the cuticles of some recent and fossil cycadean fronds. *Trans. Linn. Soc.* London Jour. (2nd Series) Botany. **8** (5).

**Thompson, W. P. 1916.** The morphology and affinities of *Gnetum. Am. J. bot.* **3**: 135-184.

———**1918.** Independent evolution of vessels in Gnetales and Angiosperms. *Bot. Gaz.* **65**: 83-90.

———**1919.** Companion cells in bast of *Gnetum* and Angiosperms. *Bot. Gaz.* **68**: 451-459.

**Traverse A. 1950.** The primary vascular body of *Mesoxylon Thompsonii. Am. J. bot.* **37**: 318-325.

**Turrill, W. B. 1959.** *Vistas in Botany.* Pergamon Press. London.

**Van Tieghem 1869.** Anatomie comparèe de la fleur femele et du fruit des Cycadees des Conifères et des Gnetaces. *Ann. Sci. Nat. Bot.* **10**: 269-304.

**Vasil, V. (Neė Negi) 1959.** Morphology and embryology of *Gnetum ula* Brongn. *Phytomorphology* 9: 167-214.

**Walton, J. 1953.** *An Introduction to the Study of Fossil Plants* Adam & Charles Beck London.

———**1964.** The Pteridosperms, Presidential address. *Trans. Bot. Soc.* Edinb. 39.

**Wardlaw, C. W.** *Embryogenesis in Plants.* Methuen & Co. Ltd. London & New York.

**Waterkeyn, L. 1959.** Etudes sur les Gnètales II, Le strobile mâle, la microsporogenèse et le gamètophyte mâle de *Gnetum africanum* Welw. *La Cellule,* 60: 1-78.

**Wettstein, R. 1935.** *Handbuch der Systemetischen Botanik.*

**Wieland, G. R. 1906.** *American fossil cycads* I. *Carnegie. Inst. Washing. Pub.* 34: 1-295.

———**1920.** Distribution and relationship of Cycadeoids. *Am. J. bot.* 7: 125-145.

**Williamson, W. C. 1873** On the organisation of fossil plants of the coal measures. IV *Dictyoxylon, Lyginodendron, Heterangium, Phil. Trans. Roy. Soc.* London. 168 B: 377-408.

**Willis, J. C. 1966.** *A Dictionary of the Flowering Plants and Ferns.* Cambridge Univ. Press.

**Wodehouse, R. P. 1935.** *Pollen Grains.* McGraw Hill Book Co., New York.

**Worsdell, W. C. 1897.** On transfusion tissue, its origin and functions in leaves of gymnospermous plants. *Trans. Linn. Soc.* London Bot. II. 5: 301-319.

# AUTHOR, NAME AND SUBJECT INDEX

## G



## H



## I



## J

## K



## L



## M



## N

,6
, 14